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Devoted to Natural History, Primarily that of the Prairie States

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Contents

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Reproduction of Upland Conifers in the Lake States as Affected by Root Competition and Light[1]

Hardy L. Shirley

CONTENTS

Introduction

A high proportion of the world's best yielding timber trees, including many species from which the highest quality lumber is sawn, reproduce with difficulty in their own shade. In ecological language they are constituents of subclimax types, which if left undisturbed eventually give way to climax types composed chiefly of shade tolerant species. To perpetuate stands of high

1 This work was carried out while the writer was assigned to the Lake States Forest Experiment Station. Suggestions for statistical treatment and simplified methods of presenting data were made by R. H. Blythe, Jr., Silviculturist. The writer wishes also to acknowledge the valuable aid of Paul Zehngraff, Associate Silviculturist, and of the many other assistants who helped carry the field and office work.

value subclimax trees is one of the most intricate silvical tasks faced by foresters.

In the tropics, the valuable teak, mahogany and Spanish cedar are crowded by a multitude of low value competitors. In temperate regions, Sitka spruce, Douglas fir and western white pine wage a losing struggle against western hemlock and firs; pitch, shortleaf, loblolly and longleaf pine are dependent upon fire, land abandonment or other major upsets to hold their own against low yielding gum, oak and other hardwoods; and white pine and white spruce ultimately give way to hemlock, balsam, or northern hardwoods. It is not surprising, therefore, that studies designed to determine satisfactory methods for reproducing intolerant tree species have occupied the attention of a large number of research workers.

In the Lake States the balance between the valuable conifers, jack pine, red pine, white pine and white spruce, on the one hand, and the low value hardwoods, aspen, birch, scrub oak and brush, on the other, is so delicate that almost any unfavorable factor may result in widespread retreat of the conifers. And once ground is lost to aspen or brush the pine forest does not necessarily reappear in the successional stages leading to the maple-basswood climax type.

CONTROLLING FACTORS—LIGHT OR ROOT COMPETITION

Among the multitude of physical and biological factors that govern the germination, establishment and growth of tree seedlings beneath forest canopies, light intensity and root competition have received greatest attention. Fricke in Europe and Toumey (50) in America directly challenged the view that light was the dominant factor. Their views have stimulated work and speculation by a number of investigators attempting to clarify the question (1, 3, 5, 13, 14, 31, 51). Many writers have studied only one factor yet drawn conclusions regarding the relative importance of both. Few have designed their experiments so that the importance of light and root competition can be evaluated separately. The conflict in opinion is well brought out by three of the more recent studies. Korstian and Coile (23) finding that soil moisture in pine stands sometimes approaches the wilting percentage, state the case for the exponents of the root competition theory as follows: "Survival of plants under forest canopies is dependent upon a complex of factors. It varies not only with climate and altitude, but very markedly with soil moisture, soil temperature, soil nutrients, light intensity, and other factors as well. Light intensity is usually subordinate in importance. * * * The increasing significance ascribed to soil moisture, with a somewhat corresponding reduction of the importance of light intensity, in forest competition and in forest succession has called for not only a reconsideration of the basic concepts of forest competition and forest succession, but also for a determination of the significant factors involved in tolerance."

The opinion that light intensity is usually subordinate in importance to soil moisture is squarely at variance with the conclusion of Gordon and Buell (17) who, working in northern Minnesota with trenched and untrenched plots, found that the advance of maple-basswood reproduction into spruce-fir stands was merely retarded by low soil moisture, but absolutely prevented by light intensity of less than 5 percent of total sunlight.

The root competition theory is further weakened by Olmstead's (30) report that in an oak-maple forest in Wisconsin, populations of herbaceous plants and survival and growth of maple seedlings, even during the drought year of 1936, showed no significant relation to root competition, but the limiting effect of low light intensity was clearly evident.

Competition by roots involves competition for available mineral nutrients and water needed for plant development. If the soil is low in moisture or in nutrient supplying capacity, dense vegetative growth is impossible, irrespective of conditions above ground. Such a statement requires no elaboration. Root competition, nevertheless, is difficult to study. In the first place, there is no direct physical means by which the intensity of root competition can be measured. It can be approximated only indirectly by measuring soil moisture, which is affected by precipitation and evaporation as well as by root intake, and by determining the amount of nutrient elements actually absorbed by the growing plant from the soil. In the second place, it is difficult to vary root competition independently of crown competition, especially in natural habitats. Live roots of trees can be eliminated from small quadrats by trenching around them, but roots of tree seedlings more often have grass, herb, and shrub roots as their competitors. This competition can be eliminated only by removing the vegetation and thereby modifying above ground competition at the same time.

Competition above ground takes the form of competition for crown space and competition for light. Some will insist that above ground competition involves light quality. This contention is not supported by physical measurements, because leaves transmit little light and show no pronounced selectivity in reflection[2] (38, 41). Light quality beneath a forest canopy is only slightly more green than sunlight. Furthermore Burns (10) has shown that when allowance is made for actual energy absorbed photosynthetic efficiency is little affected by wave length. Light intensity can be measured quite easily in the forest, and by means of artificial shades it can be varied independently of root competition. The effect of light on reproduction may therefore be more precisely evaluated than that of root competition. The experiments to be described were designed first, to determine the optimum light intensity for growth of conifer seedlings in northern Minnesota; second, to determine if and to what extent light requirements are modified by competition of roots and subordinate vegetation; and finally, to appraise the relative importance of light and root competition in the establishment, survival, and growth of conifer seedlings in brush lands, and in natural aspen, jack pine and red pine forests. Out of these studies has grown a clarified concept of tolerance, as well as basic information upon which sound silvicultural practice can be built.

CLIMATE AND SOIL OF THE REGION

The Chippewa National Forest, on which these studies were carried out, lies in north-central Minnesota at latitude 48°. Field work was confined to the original National Forest area of some 300,000 acres and to the nursery located

[2] Loomis, W. E., P. H. Carr, and H. M. Randall. Absorption of Radiant Energy by Leaves. Presented before the Gibson Island Conference on Photosynthesis. 1941.

in the village of Cass Lake. Long, cold winters often with temperatures as low as –50° F.; very short springs; warm summers with long days; early frost and snow followed by more or less prolonged Indian summers are characteristic of north-central Minnesota climate. Weather records at Bemidji, Cass Lake, Grand Rapids, and Leech Lake Dam (53) show the average annual precipitation to be 24 inches, more than half of which falls during the growing seasons. The mean annual temperature for the period of record was 39° F., and mean

TABLE 1.—Mean monthly precipitation [3] during the growing season at Cass Lake, Minnesota in 1930-36, inclusive.

Year	Mean precipitation by months		
	June	July	August
	Inches	Inches	Inches
1930	3.82	1.26	0.47
1931	3.65	3.31	1.37
1932	1.47	3.39	2.93
1933	1.45	0.56	1.72
1934	5.39	1.54	1.35
1935	4.30	5.67	3.62
1936	3.30	0.40	1.83
30-year normal	3.63	2.88	3.22

[3] Data from U. S. Weather Bureau (52).

temperature of the growing season, which averages 150 days in length, was about 62° F. (52). The period covered by the more intensive experiments, 1930-1936, was characterized by deficient rainfall during the summer months. Only one year, 1935, was free from drought (table 1). The most severe drought years, 1930, 1933, and 1936, caused widespread losses to natural vegetation and plantations.

Due to glaciation the landscape is essentially level, with gentle, almost imperceptible ridges, interspersed with numerous shallow, marshy lakes and swamps that drain into the headwaters of the Mississippi River. The soils vary from fine sands to clay loams. Cass Lake fine sand is the dominant soil throughout the study area but this borders on Nebish loam in the aspen forest. Both soils show little modification from their parent material. The loams were laid down as a till plain or ground moraine, and the sands were deposited as an outwash plain from the ice sheet (1a, 24, 25). Both major types are uniform over large areas. The conifer-producing ability of this soil and climate, together with the ease of logging afforded by level topography, are typical of the medium-to-good forest sites of the Lake States.

Establishment and Growth of Conifers in Artificial Shades

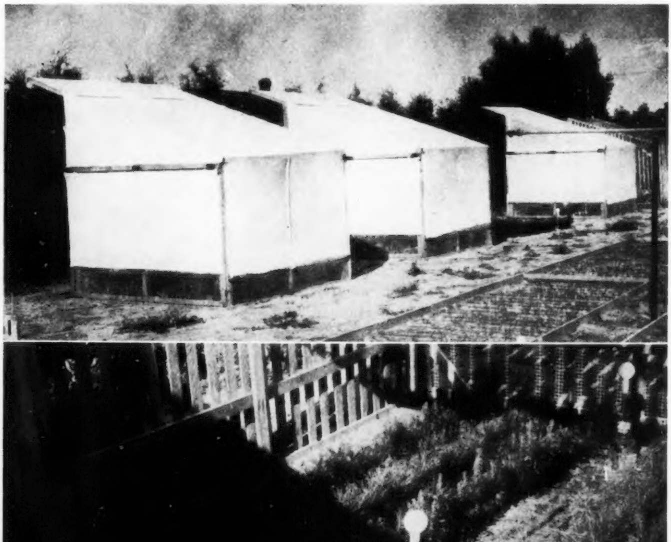
Experimental Methods and Conditions

Four shading frames were erected in the Cass Lake nursery on a section of fine, sandy soil, Cass Lake series, that had been fertilized and planted to a cover crop the preceding summer. The frames were six feet square with a sloping roof six feet high on the north and four feet high on the south. (Fig. 1). A space approximately 10 inches wide just above the ground level was cov-

ered with two-mesh hardware cloth and a similarly covered opening, shaded by an extension of the roof, was provided in the top to assure satisfactory circulation of air.

The roof and remainder of the sides of each frame were covered with one of the four shading materials, heavy muslin, light muslin, cheesecloth, and laths at a spacing of 1 lath width. A fifth bed, unshaded, was located between the light muslin and cheesecloth covered frames.

Each year on 5 to 7 cloudless days well distributed over the growing season, light intensity was measured between the hours of 9 a.m. and 4 p.m. Readings were taken at 10 to 15 different points in the cloth shades and at 20 to 50 points in the lath shade to get a reliable average. All light readings in this and subsequent experiments were taken with a device uniformly sensitive to all wavelengths of light (33) and expressed as percentages of total



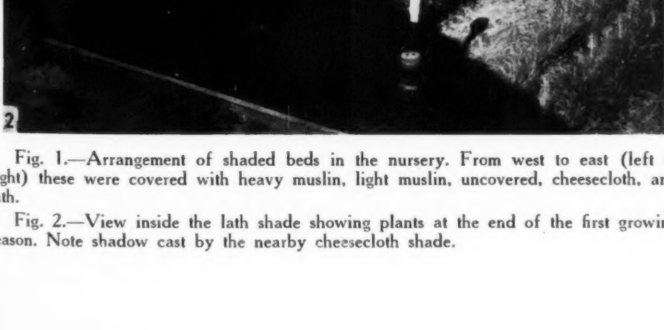


Fig. 1.—Arrangement of shaded beds in the nursery. From west to east (left to right) these were covered with heavy muslin, light muslin, uncovered, cheesecloth, and lath.

Fig. 2.—View inside the lath shade showing plants at the end of the first growing season. Note shadow cast by the nearby cheesecloth shade.

sunlight as determined by hourly readings made in the open. Light intensities averaged for each of the 4 years are given in Table 2. The two muslin shades had relatively high intensities the first year, but lower ones thereafter due to accumulation of dirt and use of heavier shading cloth. As the distance between beds was only 6 feet, shadows cast by one shade fell on another during morning and late afternoon hours. This was offset to some extent by increased light due to reflection from the opposite direction. Readings above 100 percent in the unshaded bed are due to light reflected from adjacent cloth shades, those below 100 percent to shadows cast by adjacent shades.

Weekly temperature readings of air, surface soil, and soil at 8 inches depth were made with laboratory thermometers, chiefly in the afternoons when variations due to shading were at a maximum. On cloudy days, air and soil temperatures were essentially uniform in all beds. On bright days temperatures increased with increasing light intensity, but the average temperature differences between 11 and 98 percent light were small, 1.3° C. for air, 3.2° C. for surface soil and 1.1° C. for soil at 8 inches depth.

Paired Livingston spherical atmometers were operated in each shade during the first two seasons. Because dirt and algae clogged the evaporating surfaces and rain valves functioned poorly, psychrometric readings were substituted for evaporation records during the last two years. The weekly evaporation averaged 130 cc. in 1931 and 157 cc. in 1932. Highest evaporation occurred in the unshaded bed which for the two years was respectively 27 cc. and 8 cc. above the average of the five. Variations in evaporation in the shaded beds depended as much on the degree of shelter from wind as on light intensity. Variations in relative humidity averaged less than 1 percent and showed no correlation with light intensity.

In summarizing, it can be stated that although both temperature and evaporation tended to increase with light intensity, the variations in these factors were so small compared with differences in light that their influence, judged from studies of these factors by other investigators, must have been of minor importance (20). No record was kept of soil moisture. Water was applied as needed to keep the soil moist enough for uninterrupted growth.

In early spring of 1931, two-year-old seedlings of white pine, red pine, and white spruce, and one-year-old jack pine, all grown in the Cass Lake nursery from locally collected seed, were lifted and weighed individually. Cold, rainy weather prevented root drying during this operation. After discarding seedlings weighing less than 1.2 or more than 9.0 grams fresh, the remaining ones were transplanted two inches apart in rows running east and west, which were spaced six inches apart (Fig. 2). A single species was planted in each of these rows. The rows from south to north contained red pine, white pine, jack pine, and white spruce; this series was repeated three times in each shade. A total of 102 plants of each species was planted in each shade. The original percentage of dry matter was determined on samples of each species selected from among those weighed. These percentages were applied to the fresh weights to determine the dry weight at time of transplanting (table 3).

To maintain ample growing space throughout the experiment, and to provide a sample of plants for detailed study of growth, each bed was thinned on

May 28, 1932, to 50 plants of each species; on August 1, 1932 to 25; on July 7, 1933 to 18; and on May 31, 1934 to 9. Plants removed in thinning were washed, representative individuals photographed, roots severed from tops, top and roots weighed fresh, dried in an oven and reweighed.

TABLE 2.—Percentage light intensity in shaded beds, averaged by years.

Year	Days light was measured	Light intensity in beds shaded by— Heavy muslin	Light muslin	Laths	Cheese-cloth	Not shaded
	Number	Percent	Percent	Percent	Percent	Percent
1931	5	23.8	32.8	43.6	50.6	93.0
1932	7	9.4	16.8	[5]46.6	[5]32.2	99.9
1933	5	[4]7.8	17.7	43.0	46.4	100.4
1934	5	4.6	12.8	37.9	54.5	100.2
Mean		11.4	20.0	42.8	45.9	98.4

4 Mean of 4 determinations only.
5 Mean of 6 determinations only.

Even with frequent thinnings, the slower growing species did undergo some degree of competition. In all beds, jack pine soon overtopped the others; therefore, it was necessary to remove all except the northernmost row of this species and to thin it to four plants in each bed before the beginning of the fourth growing season. Only white pine, the slowest growing, was suppressed enough to interfere significantly with its growth, and this occurred only in 46 and 98 percent light. The net effect of crowding was to reduce rather than to accentuate the differences in plants from the 5 beds.

TABLE 3.—Fresh and dry weights of seedlings at time of transplanting into shaded beds in nursery.

Species	Fresh Weight Mean	Fresh Weight Standard Deviation	Dry Weight[6] Mean	Dry Weight[6] Standard Deviation
	Grams	Grams	Grams	Grams
Red pine	4.55	1.49	1.73	.57
White pine	4.04	1.45	1.69	.61
Jack pine	3.61	1.41	1.41	.55
White spruce	3.54	1.53	1.63	.70

6 Calculated from fresh weight by applying average percentage of dry matter.

HEALTH AND SURVIVAL

Within nine weeks after transplanting, it was possible to detect unfavorable symptoms among the plants in the lowest light intensity. The foliage of white spruce became glaucous blue, while the new needles on white pine were distinctly chlorotic. Foliage color of jack pine and red pine was normal but the

new needles were slender and the stems thin. Similar, though less pronounced symptoms, were detected in 20 percent light towards the close of the experiment. Plants in the other three beds appeared normal throughout. The color was deep green and growth rapid. Jack pine produced cones in all shades. During the last two years, however, it showed a distinct decline in vigor in 11 percent light, followed by a corresponding increase in mortality. Plants in 11 and 20 percent light that grew next to the ventilators were taller and more vigorous than those in the center of the beds. This difference in size was prob-

TABLE 4.—Transplant mortality in nursery beds, by species and light intensities.

Light Intensity	Year[7]	Mortality by species: Red pine	White pine	Jack pine	White spruce	Total
Percent		Number	Number	Number	Number	Number
	1931	6	39	15	4	64
	1932	11	15	9	3	38
11	1933	0	2	2	1	5
	1934	0	0	1	0	1
	Total	17	56	27	8	108
	1931	3	14	13	0	30
	1932	1	6	3	2	12
20	1933	2	3	0	0	5
	1934	0	0	0	0	0
	Total	6	23	16	2	47
	1931	1	0	1	1	3
	1932	0	0	0	0	0
43	1933	0	0	0	0	0
	1934	0	0	0	0	0
	Total	1	0	1	1	3
	1931	0	3	1	2	6
	1932	0	0	0	0	0
46	1933	2	3	0	0	5
	1934	0	0	0	0	0
	Total	2	6	1	2	11
	1931	7	1	2	0	10
	1932	0	0	0	2	2
98	1933	0	0	0	0	0
	1934	0	0	0	0	0
	Total	7	1	2	2	12

[7] From beginning of one growing season to beginning of next. The approximate numbers alive of each species in each shade by growing seasons were: 1931—102; 1932—50; 1933—25; 1934—18, except for jack pine, which was thinned to 4 plants per bed on July 7, 1933.

ably due chiefly to the increased light coming in through the ventilator since mutual competition for soil moisture and nutrients was far less intense in these two intensities than in 43, 46 and 98 percent light where the border effect was not noticeable, and where the plants after the first year were too tall to benefit appreciably from light coming through the ventilators.

Transplant mortality as determined by a count made each spring and fall was relatively high during the first two years, particularly in 11 percent light, and to a less extent in 20 percent light. Total losses by beds are given in table 4. Reducing the light to 46 and 43 percent had no important effect on mortality, whereas reducing it to 20 percent caused an average mortality of 12 percent, and with only 11 percent light, the losses were 27 percent. White pine had the greatest losses both in 11 and 20 percent light, but differed little from the other species in the better lighted beds. Mortality in jack pine was also high in these low light values. Thinned to four plants per bed on July 7, 1933, three of the remaining four plants in 11 percent light died during the following winter and summer. The high survival of white spruce in the two lowest light intensities strongly suggests that this species differs significantly in physiological requirements from the three pines. Grouping together the total losses in 11 and 20 percent light, we find them to be white spruce 10, red pine 23, jack pine 43, and white pine 79. Approximately 70 percent of the mortality of white pine and red pine occurred during the winter, whereas losses of spruce and jack pine were about equal in winter and summer. This suggests that cold resistance of red and white pine is reduced by low light intensities. Just why jack pine and white spruce were not similarly affected is unknown unless they have greater cold resistance or can become adjusted to cold more rapidly than red and white pine.

GROWTH IN HEIGHT AND DRY WEIGHT

Height at the end of each growing season is shown in Fig. 3. In autumn of the first year spruce and jack pine averaged about 0.5 foot in height, red pine 0.4 and white pine 0.3. Little difference in height was evident regardless of the amount of light. This indicates that first year growth in height of newly planted conifers is made largely at the expense of food stored during the preceding year, and therefore, it cannot be used as an index of the excellence of growing conditions. Beginning with the second year the height increment in 11 percent light is a resultant of two opposing factors, the etiolating effect of low light intensity which tends to stimulate stem elongation, and the reduced food supply which limits all growth. The starvation effect became dominant in jack pine during the second year and in the other species during the third year. Light intensities of 43 and 46 percent, which are adequate to prevent the starvation effect, allowed maximum stem elongation. Under the conditions of this experiment an intensity of about 45 percent appears to be optimum for growth in height. However, since soil conditions in the nursery were known not to be optimum for growth of these species, this value cannot be accepted as final. It is particularly important to note that jack pine was tallest of all species regardless of light intensity. This indicates that wherever

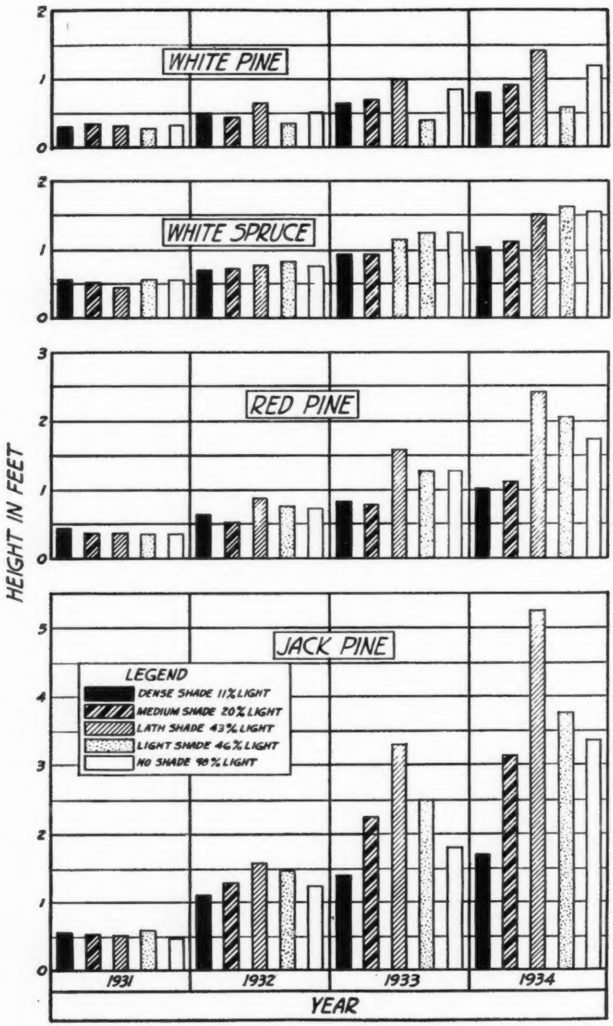


Fig. 3.—Growth in height of conifers in shaded beds in the nursery.

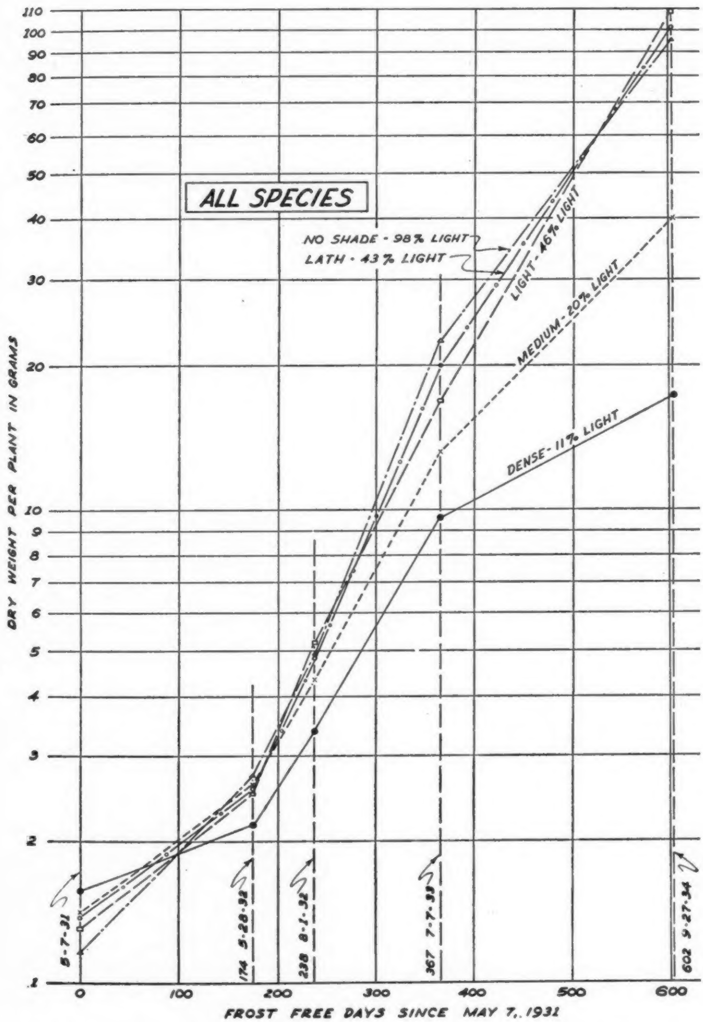


Fig. 4.—Dry weight as affected by light intensity—all species grouped together. Light intensities are: dense shade, 11 percent; medium shade, 20 percent; lath shade, 43 percent; light shade, 46 percent; no shade, 98 percent.

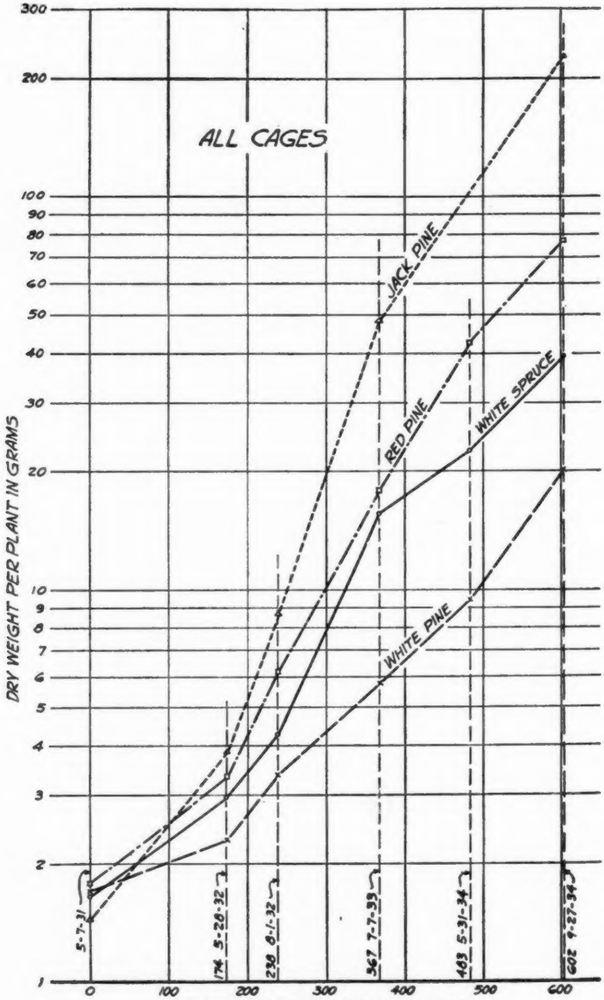


Fig. 5.—Dry weight of different species—plants from all shades grouped together.

light conditions are adequate for survival, jack pine will outgrow the other species. White spruce, which is the slowest growing under normal conditions, was least affected in height by shading. The slow growth of white pine in 46 percent light was the result of overtopping by red and jack pine. Height growth of the three pines was greater in the lath shade than in the cheesecloth shade which had approximately the same light intensity. It is possible that the variable light intensity produced by the lath shade is more favorable for height growth than the uniform light of the cheesecloth shade. However, little significance is attached to this since it was not accompanied by an increase in dry weight.

The average dry weights at each of the four thinning dates and at the close of the experiment are shown graphically for all species in Fig. 4, and for all shades in Fig. 5. In both of these figures the positions of the sampling dates are determined by the number of frost-free calendar days from date of planting. Ordinates are shown on a logarithmic scale. The dry weight attained in 43, 46, and 100 percent light was approximately equal. Plants in 11 percent light had fallen behind the others at the time of the first thinning; this disparity increased at each succeeding date. Those in 20 percent light showed a similar trend starting with the second thinning. At the close of the experiment the average dry weight per plant was roughly in direct proportion to the light intensity over the range of 11 to 46 percent light.

After one season's growth the species had become arranged in order of increasing weight as follows: white pine, white spruce, red pine and jack pine (Fig. 5). The disparity among species increased at later dates but the order of increasing size remained unchanged. At the close of the experiment the dry weights were in the ratio 1:2:4:11.

TABLE 5.—Dry weight of plants after 4 years' growth in shaded nursery beds.

Shade	Light intensity	Average dry weight per plant by species: White pine[8]	White spruce	Red pine	Jack pine
	Percent	Grams	Grams	Grams	Grams
Dense	11	16	20	26	26
Medium	20	20	31	36	113
Lath	43	31	40	94	349
Light	46	9	49	108	374
None	98	24	58	121	280

[8] Due to crowding by other species, the dry weight of white pine in the beds having 46 percent and 98 percent light is considerably less than would normally be expected.

The final dry weights are shown in table 5. There was little difference among species in 11 percent light intensity, which proved to be unfavorable for all. In 20 percent light the weights varied from 20 grams for white pine to 113 for jack pine or a range of from 1 to 5.6; in the lath shade and unshaded bed the range was approximately twice as great. Jack pine exceeded the others

in dry weight in intensities of 20 percent and higher. This merely reflects the known tendency of this species to grow more rapidly in early life than associated conifers. However, the ability of this species to maintain an advantage over all others except red pine in 11 percent light intensity where more than 25 percent of the plants died was not anticipated. It is significant that jack pine with a decrease in light intensity from 98 to 11 percent underwent a 91 percent reduction in total dry weight, red pine a 78 percent reduction, and white spruce only a 66 percent reduction.

STOCKINESS AND ROOT DEVELOPMENT

It was perfectly evident that the plants in the higher light intensities were more vigorous and sturdy than those in medium and dense shade. This was expressed in better color, thicker needles, stiffer and thicker stems and more branches. In order to get an arithmetical expression of this character the dry weight of the top was divided by the length of the stem, or in other words the average weight per foot of height was found. These values are given in table 6.

All four species had a low ratio of dry weight to height in 11 percent light. This ratio increased with increasing light up to 98 percent light for red pine and white spruce, and to 46 percent light for jack pine. White pine attained higher values in 20 and 43 percent light where it was least crowded by the other species.

TABLE 6.—Stockiness of plants harvested on September 27, 1934, as affected by shading.

Shade	Light intensity	Average dry weight of top per foot of stem length			
		Red pine	White pine	Jack pine	White spruce
	Percent	Grams	Grams	Grams	Grams
Dense	11	22	15	15	12
Medium	20	27	17	31	22
Lath	43	34	17	56	16
Light	46	44	12	86	25
None	98	58	15	69	30

The increase in vigor and stockiness with increasing light intensity is also quite apparent from the photographs taken at the time of final harvest (Fig. 6). One argument for growing young trees under shade is that shading reduces the number of branches. Reference to the photographs will show that the relative number and size of branches appears to be about the same for all shades. The chief difference is that the internodes, relative to the size of the plant, are longer in the dense and medium shades.

Root development increased with increasing light similarly to dry weight, table 7. The three pines attained essentially the same root development in 43

or 46 percent light as in full sunlight, but spruce attained greatest root development in full sunlight. The better development of roots in the higher light intensities was quite distinctly evident at the end of the first growing season.

Shading did not produce topheavy plants, as might have been expected. The ratios of tops to roots on a dry weight basis were essentially uniform for a single species regardless of the light intensity. For jack pine these ratios

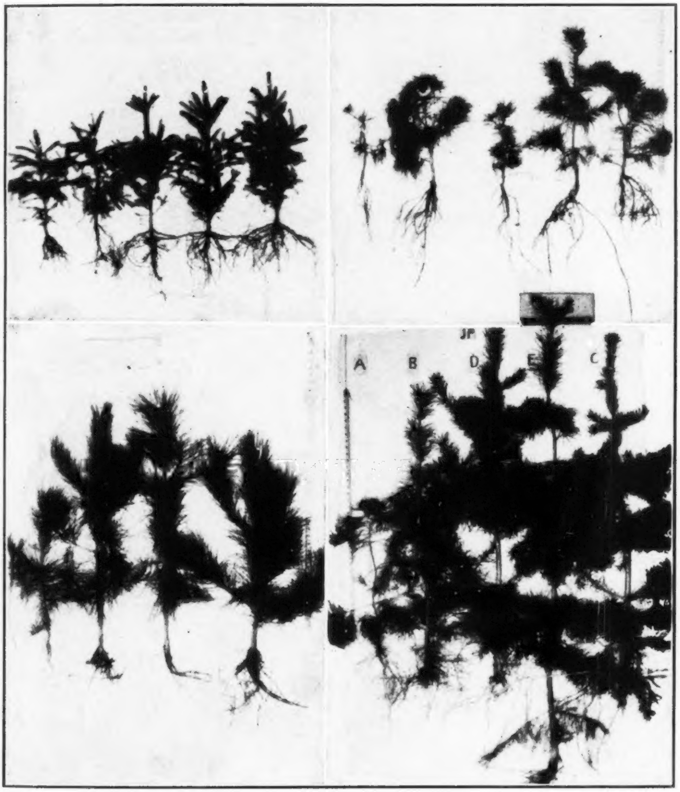


Fig. 6.—Median plants at the time of final harvest. Upper left red pine, upper right white pine, lower left white spruce, lower right jack pine. Plants of each species are arranged from left to right as follows: dense shade (11 percent light), medium shade (20 percent light), light shade (46 percent light), lath shade (43 percent light), no shade (98 percent light).

were: 4.0, 4.0, 4.0, 4.4, 4.0 for 11, 20, 43, 46 and 98 percent light respectively. Top-root ratio is, perhaps, not a proper measure of balance

TABLE 7.—Dry weight of roots as influenced by light intensity.

Shade	Light intensity	Dry weight of roots per plant			
		Red pine	White pine	Jack pine	White spruce
	Percent	Grams	Grams	Grams	Grams
Heavy	11	3.4	3.5	4.5	4.3
Medium	20	5.0	4.8	16.2	6.2
Lath	43	11.8	6.5	54.8	8.1
Light	46	17.6	2.4	52.0	8.8
None	98	19.0	6.0	49.8	12.0

between root and top when the plants vary greatly in size, because stem tissue increases more rapidly in weight with size of tree than root tissue.

SUMMARY, ARTIFICIAL SHADES

Survival in 43, 46 and 98 percent light was approximately equal, averaging 98 percent for all species. In 20 percent light, survival was 90 percent, and in 11 percent light, 73 percent. The fact that losses during winter were greater than during summer suggests that shading reduces resistance to cold. Spruce survived much better than the pines in 11 and 20 percent light, an indication of differences in physiologic requirements. Indefinite survival of pines, at least of jack pine in 11 percent light is questionable.

Maximum height of all species occurred at about 43 percent light. Maximum dry weight of red pine and white spruce occurred in full sunlight, of jack pine and white pine in 46 and 43 percent light. Root development was in proportion to top development in all light intensities. Stockiness, as determined by ratio of weight to height, increased in general with light up to about 45 percent intensity. The extent to which survival and growth was reduced from the optimum by low light intensities may be used as a criterion of relative light requirements. On this basis the species increase in light requirement in the order jack pine, red pine and white spruce. As a result of extraneous influences, the data on white pine are inconclusive.

From this experiment it seems safe to conclude that where all other growth factors are favorable, pines require in the neighborhood of 20 percent light for satisfactory survival and 43 percent for optimum survival. Spruce requires 11 percent light for satisfactory survival and 20 percent for optimum survival. Optimum growth of all species can occur only in light of 43 percent or greater. These conclusions will next be tested by observing the growth of the same species when subjected to the competition of vegetation in an aspen forest.

Establishment and Growth of Conifers as Influenced by Shade and Root Competition of Aspen

EXPERIMENTAL METHODS AND CONDITIONS

Competition in the aspen forest was separated into three main components; namely (1) that caused by the aspen overstory alone with root competition eliminated by trenching, and under-vegetation by weeding; (2) that caused by the aspen overstory with root competition present but under-vegetation weeded out; and (3) that caused by root and top competition of both aspen overstory and the under-vegetation. For each condition three light intensities were maintained by cutting in the overstory, while the under-vegetation afforded three additional intensities. This provided an opportunity to vary light intensity with root competition eliminated, with root competition of the overstory only, and with root competition of both overstory and undergrowth.

The aspen stand chosen for this study was 43 years of age in 1929, and was composed of trembling aspen with subordinate stems of bur oak and red maple. Sample plots one-quarter acre in size, numbers 37, 38, and 39, were laid out where the stands were essentially uniform in size and density. From Plot 37 all trees were cut, and on Plot 38, 36 percent of the initial basal area was cut. Plot 39 remained uncut (Fig. 7). In each case cutting extended 25 feet beyond the border of the plot. All logging debris was removed from the plots by hand so as to disturb the soil and undergrowth as little as possible. The site index, number of trees, basal area, and volume before and after cutting, and five years after cutting, are shown in table 8. Compared with stands

Fig. 7.—High quality 50-year-old aspen, Plot 39. Photographed in 1936. Conifers on weeded quadrats are shown in the foreground.

shown in normal yield tables, Plots 37 and 39 were understocked in number of trees, but practically normal in basal area, whereas Plot 38 was essentially normal in both number of trees and basal area. Seed trees of red and white pine were scattered around the periphery of all plots and natural seedlings, few in number and less than one foot in height, were present. Following cutting, a vigorous growth of aspen sprouts sprang up on the clear-cut plot. These averaged 50,000 per acre at the end of their first growing season, and 3.4 feet in height. By the ninth year, the number had decreased to 6,300 per acre, and the average height increased to 17 feet. Root sprouts on the other two aspen plots were infrequent and lacking in vigor; most of them died before the experiment was concluded. The subordinate vegetation consisted of a layer of tall

Fig. 8.—Ferns and shrubs forming understory in 44-year-old aspen, a control quadrat on the uncut plot photographed in 1930.

shrubs, and a layer of low shrubs and herbaceous plants. The most conspicuous tall shrubs were beaked hazel, American hazel, round-leaved dogwood, and round-leaved shadblow (Fig. 8). The most common low shrubs and herbs were brake, interrupted fern, dwarf bush honeysuckle, wild sarsaparilla, and big-leaved aster.

The soil, Nebish loam series, had a weakly defined podsolized profile with indistinctly differentiated horizons. Undecomposed leaf litter one-half to one inch in thickness underlain by a two-inch layer of decomposing organic matter was common to the soil of the three plots. Below the humus or A-1 horizon a dark gray, very fine sandy loam five to ten inches in thickness, interspersed with charred organic fragments formed the A-2 layer. This changed rather gradually into a reddish brown, very fine sandy loam, the B horizon, that extended to the underlying clay. The clay occurred at 30 inches depth on the 36 percent cut plot, 22 inches on the clear-cut plot, and 24 inches on the uncut

TABLE 8.—Stocking and site index of variously treated plots in a 43-year-old aspen stand.

Plot No.	Treatment and date of measurement	Site index[11]	Stand per plot		
			Trees	Basal area	Volume
			Number	Square ft.	Cubic ft.
37	Clear-cut, 1929				
	Before cutting	77	102	32.6	950
38	36 percent cut, 1929				
	Before cutting	71	151	33.7	970
	After cutting [9]		85	21.5	615
	1935		75	22.8	650
39	Uncut				
	1929	73	105	30.4	876
	1935		80	29.2	843
	Normal 43-year-old stand[10]	73	156	32.0	823
	Normal 48-year-old stand	73	121	34.2	950

9 In addition to aspen and other hardwoods plot 38 had one 27-inch red pine, with a basal area of 4 sq. ft. (3.98) in 1929. In 1935 this red pine was 27.2 inches with a basal area of 4.03 sq. ft., volume approximately 148.00 cubic feet.

10 Represented by yield tables constructed by S. R. Gevorkiantz (8).

11 Site index is the height of the average dominant tree at 50 years of age.

plot. The clay was slightly mottled, granular in structure and contained aspen roots. No distinct division occurred between the B and C horizons. Samples of soil were analyzed in the laboratory for percentage of sand, silt, and clay, and for wilting coefficient, table 9. The soil of the partially cut plot proved to be more sandy than on the other two, which probably accounts in part for the lower site index on this plot.

TABLE 9.—Physical characteristics of soil on the aspen plots.

Treatment	Wilting[12] coefficient	Soil components[13]		
		Combined sand	Conventional silt	Conventional clay
	Percent	Percent	Percent	Percent
Clear-cut	5.0	69.1	24.6	6.3
36 percent cut	3.7	80.3	14.6	5.0
Uncut	5.4	71.9	21.1	7.0

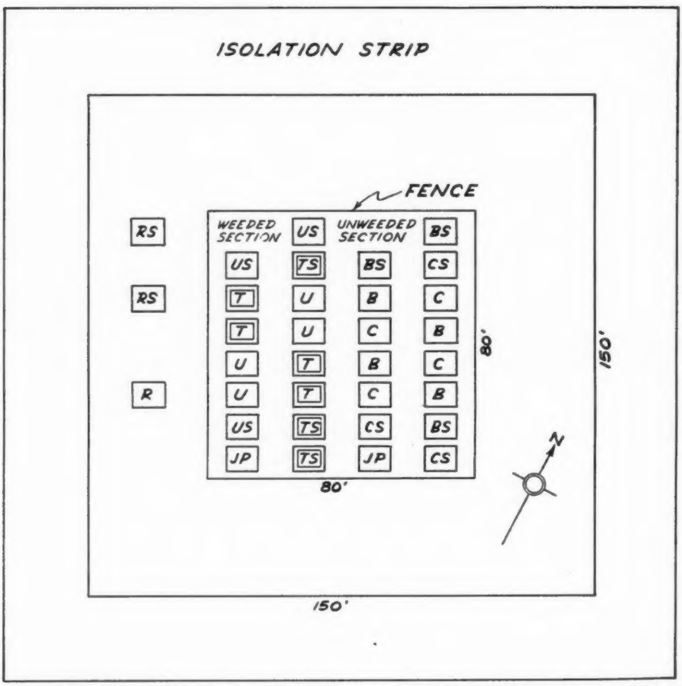
12 Wilting coefficient $= \frac{\text{Moisture equivalent}}{1.84}$

13 Determined by Bouyoucos hydrometer method (6, 7).

A total of 16 quadrats 10 feet square were laid out on each plot so as to include no live trees or newly cut stumps. From 8 of these all natural vegetation was excluded by periodic weeding. Weeds were pulled by hand for the first two years while the humus layer remained intact; thereafter, they were removed with a garden hoe. Four of these eight quadrats on each plot were surrounded by a trench 30 inches deep which was refilled after the roots had

been trimmed flush with the sides. The trenches were reopened in the spring of 1932, the fall of 1933, and in the spring of 1936. On four quadrats the herbs and shrubs were killed by burning with a gasoline brush-burning blow-torch applied so as to give the effect of a light surface fire. The final set of four quadrats was left as controls, with the under-vegetation intact. The 16 quadrats were grouped near the center of each plot and so arranged that trenched alternated with untrenched, and burned with controls. Isolation strips of 4 or more feet were left between trenched and untrenched quadrats. An additional set of quadrats treated by the four methods was reserved for direct seeding.

The above quadrats were inclosed within a fence erected to exclude deer and rabbits. Though animals occasionally entered the enclosures they were



T- TRENCHED AND WEEDED
U- UNTRENCHED AND WEEDED
B- BURNED, NOT WEEDED
C-CONTROL, NOT BURNED, WEEDED OR TRENCHED
R- EXPOSED OUTSIDE FENCE
S- SEED SPOTS
JP- JACK PINE QUADRATS

Fig. 9.—Diagram showing arrangement of seed spots and planted quadrats in each plot.

chased out before doing appreciable damage. Additional quadrats to be planted and seeded corresponding to the control treatment were located outside the fence. The general arrangement on each plot is shown in Fig. 9.

In the autumn of 1929, 25 two-year-old seedlings of red pine and white spruce were planted on each quadrat. These were supplemented in the autumn of 1930 by an additional 25 two-year-old white spruce, and 25 two-year-old white pine. At the same time, all initial losses were replaced. This required complete replacement of red pine on burned and control quadrats of the uncut plot, and of white spruce on weeded quadrats where the aspen was clear-cut. The dry weight of the seedlings averaged from .5 to .8 grams at the time of planting. Planting holes were prepared by making an L-shaped cut through the duff and humus, which was disturbed as little as possible. The planted trees were set one foot apart in each direction, and mechanically distributed so that two individuals of the same species were not adjacent to one another in the rows. The trees planted on the quadrats will hereafter be referred to as transplants, to distinguish them from trees grown from seed on the plots to be referred to as seedlings. It was originally intended that jack pine should also be planted on each quadrat, but since no stock was available, use of this species was deferred until the spring of 1933 when 20 trees of 1-0 stock were planted on weeded but not trenched quadrats, and 20 on control quadrats. During the growing season, all plots were visited weekly to measure physical factors and to determine if weeding was required to keep trenched and untrenched quadrats free from aspen suckers, shrubs, and herbs. Height measurements were taken each autumn and survival counts made each spring and fall. Whenever mutual crowding became important, which again affected white pine more than the other species, the plants were thinned, those removed being used for dry weight determinations. The sampling procedure used in the nursery shades was followed. Due to heavy mortality on unweeded quadrats the number sampled from these was smaller, and sampling had to be discontinued earlier than on weeded ones. Final sampling on the latter occurred in 1935, leaving three of each species to remain indefinitely.

On additional quadrats treated by the four methods, 30 seed spots one foot square were scalped free of sod and litter, and 10 each sown in the spring and again in the fall of 1930 to red pine, white pine, and white spruce. Each spot was sown with approximately 15 viable seed. Establishment was poor both times; consequently the seedlings were removed and the spots resown in the spring of 1932. This time the soil was spaded and worked down, seed sown and covered, soil dressed with aluminum sulphate, and each spot protected by a rodent proof screen; excellent success resulted. During the germination period counts of seedlings emerged, and those dying from heat injury, damping off, insect attack or other causes were made weekly. Thereafter, seedlings were given the same type of care and subjected to the same survival counts, height measurements, thinning and sampling techniques given transplants.

THE PHYSICAL ENVIRONMENT

Light intensity measurements were taken at 24 marked stations four or more times each summer. Readings were taken at a height of 4 feet on trenched and untrenched quadrats and at 2 inches on burned and control quadrats. Yearly averages showed minor variations, due in part to errors in measurement, but largely to differences in canopy density resulting from growth on the one hand, and mortality on the other, table 10. The six-year average is essentially equal on the unweeded sections of the clear-cut and uncut plots, and very closely approximates the light intensity in the heavy muslin nursery shade. It will also be noted that weeded quadrats on the uncut plot and unweeded quadrats on the 36 percent cut had essentially the same light intensity as the light muslin nursery shade, though they differed greatly from it and from one another in root competition.

Temperatures of the air, surface soil, and soil at 8 inches depth were taken with laboratory thermometers once each week throughout the growing season. None of the temperatures measured was high enough to cause heat lesions on young seedlings. Deviations from the daily mean of all readings were computed for each plot and quadrat treatments. Summaries of these deviations

TABLE 10.—Yearly average light intensity on weeded and unweeded quadrats in aspen plots.

Plot and quadrat treatment	Light intensity by years						
	1930	1931	1932	1933	1934	1936	Mean
	%	%	%	%	%	%	%
Clear-cut							
Weeded	100	100	100	100	100	100	100
Not weeded		18.0	12.0	9.0	14.7[14]	9.1	12.6
36 percent cut							
Weeded	32.0	43.0	31.0	34.0	34.3	42.1	36.1
Not weeded	41.0	19.0	21.0	15.0	16.9	23.0	22.6
Uncut							
Weeded	23.0	18.0	20.0	26.0	28.3	13.4	21.4
Not weeded	14.0	13.0	12.0	8.0	22.3	8.3	12.9

14 Some sprouts were broken by windstorm.

averaged for four years are given in table 11. Highest temperatures for each treatment occurred on the clear-cut plot and lowest temperatures on the uncut plot. The surface soil of trenched quadrats on both plots having an overstory consistently showed a slightly lower average temperature during the growing seasons than that of untrenched quadrats. This is probably the result of higher moisture conditions which prevailed on these quadrats for a portion of each year. Soil temperature at 8 inches shows little difference between trenched and untrenched quadrats. Unweeded quadrats had consistently lower temperatures than weeded ones. Inasmuch as the temperature coefficient for photosynthesis is probably about 1.4, even the maximum temperature difference, 4.5° C. could scarcely account for more than an 18 percent increase in growth

rate. Compounded over a 4-year period this would account for plants on weeded quadrats of the clear-cut plot having not more than twice the dry weight of those from unweeded quadrats of the uncut plot. Their actual dry weight exceeded by 27 times that which could be accounted for on the basis of temperature differences.

Weekly evaporation from Livingston spherical atmometers averaged during the years 1930-1932, 79, 82, and 70 cc. respectively for the clear-cut, partially-cut, and uncut plots. Psychometric measurements during 1933 and 1934 indicated that relative humidity averaged 2.3 percent higher on the uncut and clear-cut plots than on the partially-cut plot. The latter was located about 300 feet from the west edge of the forest. Humidity was doubtless lowered by nearness to the open area. On all three plots the humidity was higher on the unweeded portions, varying from .2 percent higher on the clear-cut plot to .9 percent on the partially-cut plot, at or below the level of the undergrowth. Individual weekly determinations of both evaporation and relative humidity indicated that differences among plots were relatively small and by no means always consistent. Hence although the final averages may represent real differences, these are so small that they are not likely to affect appreciably the growth of conifers planted on the plots.

TABLE 11.—Temperature variations in aspen plots.

Plot and quadrat treatment	Av. deviation from daily mean[15]		
	Air temperature	Soil temperature (surface)	Soil temperature (8″ depth)
	°C	°C	°C
Clear-cut	+ 1.2		
Weeded			
Trenched		+ 2.8	+ 1.9
Untrenched		+ 2.7	+ 1.5
Not weeded			
Burned and control		— 1.2	— 1.0
36 percent cut	— 0.2		
Weeded			
Trenched		+ .1	+ .2
Untrenched		+ .6	.0
Not weeded			
Burned and control		— 1.3	— .8
Uncut	— 1.0		
Weeded			
Trenched		— 1.4	— .3
Untrenched		— .6	— .5
Not weeded			
Burned and control		— 1.7	— 1.0

15 Basis: records taken weekly throughout the four growing seasons from 1931 to 1934.

Samples consisting of exactly 50 cc. of mineral soil in place were taken for moisture determination each week during the growing season by driving into

TABLE 12.—Available moisture content of soil during dry periods.

Plot and quadrat treatment	Available soil moisture [16]															
	1930				1931			1932			1933			1936		
	August				July	Sept.		July	August		July		August	August		
	4	11	18	25	27	8	14	15	8	22	17	31	21	7	13	Mean
Clear-cut		%				%			%			%			%	%
Weeded																
Trenched	14.5	14.6	11.9	8.4	18.0	13.0	14.0	11.9	10.0	3.3	3.1	–2.0	1.4	8.0	7.4	9.2
Untrenched	8.9	7.1	3.4	.9	12.0	13.0	12.0	.0	10.0	1.5	4.1	2.2	–1.0	6.6	5.8	5.8
Not weeded																
Control					12.0	12.0	11.0	2.0	2.5	1.4	4.1	3.1	2.6	3.4	6.2	5.5
36 percent cut																
Weeded																
Trenched	7.5	10.8	3.7	1.3	9.3	2.3	6.3	3.9	2.9	2.2	3.7	1.9	4.5	2.9	1.8	4.3
Untrenched	7.9	1.4	–.2	.3	11.3	.3	2.3	3.3	1.5	1.7	.1	3.7	2.5	1.2	1.9	2.6
Not weeded																
Control					2.3	2.3	2.3	3.7	4.2	.5	1.3	2.3	3.0	4.8	3.8	2.8
Uncut																
Weeded																
Trenched	3.6	.9	1.0	2.7	3.6	1.6	1.6	5.0	6.4	2.1	2.0	6.6	2.4	5.8	10.3	3.7
Untrenched	–1.2	.1	–3.2	–1.8	7.6	.6	2.6	.0	2.0	1.0	–1.6	2.4	1.2	3.8	2.9	1.1
Not weeded																
Control					.6	1.6	–.4	–.5	–.1	.5	....	.4	.3	1.0	3.0	.6

16 Available moisture = percentage moisture by weight minus wilting percentage.

the soil just beneath the humus layer an accurately machined cylinder of 50 cc. capacity, the height of which approximately equaled the diameter. The sample was weighed, dried to constant weight at 105° C. and reweighed. Moisture content was expressed on both a volume and dry weight basis. Separate samples were collected from trenched, untrenched, and control quadrats from each plot. During wet periods there was little difference among the plots or treatments. When a light shower followed a dry period the clear-cut plot showed higher moisture content because there was no interception by crowns. These variations may be dismissed as of minor importance. Only during prolonged dry periods when the soil moisture approached the wilting percentage were the differences due to plot and quadrat treatment significant and more or less consistent, table 12. At such periods soil on trenched quadrats had the highest moisture content of all. Lowest values occurred on the control quadrats of the uncut plot where both understory and overstory made demands on the soil. On the partially-cut where the under-vegetation was less aggressive, little difference existed between the control quadrats and the untrenched—weeded quadrats. In 1933, when the trees were quite crowded on the weeded quadrats of the clear-cut plot, the soil moisture on these also became critically low.

ESTABLISHMENT, SURVIVAL AND GROWTH OF SEEDLINGS

Germination of pine was somewhat better on the clear-cut plot than on the partially-cut and uncut plots, whereas best germination of spruce occurred on the uncut plot. Quadrat treatment had no significant effect on germination in any case. White pine with a germination percentage of 87 as opposed to 99 for spruce and red pine survived better, both in summer and winter than the others. At the end of the second season survival by species was: white pine, 80 percent; white spruce, 69 percent; and red pine, 68 percent. Greatest difference in survival resulted from quadrat treatment. This alone was significant at the end of the third year when the averages were: trenched, 89 percent; untrenched, 91 percent; burned, 23 percent; and control, 14 percent. Differences of 27 percent are significant at the 1 percent level (15).

Dry weight per seedling in 1932 averaged .07, .05, and 0.1 gram respectively for clear-cut, partially cut, and uncut plots. After three growing seasons losses were so great on the unweeded quadrats that only a few were available for dry weight analyses. As the differences among species were not great and since all three showed the same general trends, the results given in table 13 are averaged for all species. The effect of competition on increase in dry weight is equally as striking as on survival. With root competition eliminated, seedlings in 21, 36, and 100 percent light respectively attained dry weight of 0.12, 0.17, and 1.35 grams; with root competition present they attained in 13, 21-23, 36 and 100 percent light respectively, .03, .08, .11 and 1.00 grams. Dry weight was essentially the same in equal light intensities whether the competition resulted from a dense aspen overstory only or a combination of a thinned aspen overstory with an understory of shrubs and herbs. The effect of surface burning on seedling weight disappeared after the first year.

TABLE 13.—Dry weight of 3-year-old seedlings as affected by light and root competition.

Quadrat treatment	Light intensity by plots			Dry weight per seedling by plots		
	Clear-cut	36 % cut	Uncut	Clear-cut	36 % cut	Uncut
	Percent	Percent	Percent	Grams	Grams	Grams
Trenched	100	36	21	1.35	0.17	0.12
Untrenched	100	36	21	1.00	.11	.08
Burned	13	23	13	.03	.07	.03
Control	13	23	13	.02	.08	....

HEALTH AND SURVIVAL OF TRANSPLANTS

Estimates of the health and vigor of transplants were taken twice annually and also at each sampling date. However, these revealed little not brought out more convincingly by mortality percentages, and by height and dry weight measurements. During the first season it was possible to detect a slight improvement in transplants on burned over those on control quadrats of the same plot. This difference soon disappeared as the herbs and shrubs on burned quadrats sprouted up and overtopped the conifers. Inasmuch as no important differences showed up in mortality, height, dry weight, or stockiness, plants on burned and control quadrats will be grouped together as a single control in most of the discussion to follow.

Mortality was heaviest during the first two years after planting. Although losses were due in part to the shock resulting from transplanting, they were caused largely by the very dry weather conditions which prevailed during these years, particularly during the summer of 1930. As in the nursery shades spruce losses were about equally divided between summer and winter seasons, but pine losses were heavier in winter. Smothering by leaves was a much more common cause of death among pines than spruce.

The mortality by species, quadrat treatments, and plot treatments, occurring between the spring of 1931, when final replacements were made, and the fall of 1934, were analyzed by the variance method (45). Differences due to species, quadrat treatments, plots, and the species-treatment interaction were significant at the 1 percent level. The average mortality by plots was:

clear-cut	39.1 percent
36 percent cut	12.5 percent
uncut	20.7 percent

Differences of 13.4 percent were significant at 1 percent level. Mortality was heavier on unweeded quadrats than on weeded quadrats though differences between trenched and untrenched or burned and control quadrats were slight, table 14. White spruce losses were significantly less than those of the two pines. Significance of the species-quadrat treatment interaction was due to the fact that mortality of red and white pine was much less on weeded quadrats than on unweeded quadrats, whereas mortality of white spruce was little in-

fluenced by competition of undergrowth. By grouping burned and control treatments together, we find mortality to average by species, red pine, 62.5; white pine, 37.3; and white spruce, 13.3 percent with each differing significantly from the other two. Heavy mortality in the clear-cut plot was due at first to losses on weeded quadrats exposed to the heat and drying action of the sun, and in subsequent years to the losses on control quadrats resulting from heavy shading. These data support the conclusion from the nursery study that 11 to 13 percent light is inadequate for satisfactory survival of red and white pine.

Between the fall of 1934 and the fall of 1938, losses on weeded quadrats averaged by plots: clear-cut—3 percent, 36 percent cut—8 percent, uncut—3 percent. No significant difference occurred among species or between trenched and untrenched quadrats. Losses on control quadrats for the same period were: red pine—26 percent, white pine—33 percent, and white spruce—21 percent. Losses to red and white pine were greatest on the clear-cut plot, and least on the uncut; losses to spruce were approximately equal on all three plots. The survival of trees exposed to rabbit browsing was approximately the same as that of protected controls on plots with an overstory, but lower on the clear-cut plot. Spruce withstood browsing much better than pines.

TABLE 14.—Mortality percentages of conifers planted in aspen plots as influenced by treatment.

Quadrat treatment	Mortality percentages,[17] by species			
	Red pine	White pine	White spruce	Mean
	Percent	Percent	Percent	Percent
Weeded				
Trenched	7.7	12.7	6.0	8.8
Untrenched	9.7	15.0	11.7	12.1
Not weeded				
Burned	64.3	40.7	14.0	39.7
Control	60.7	34.0	12.7	35.8
Mean	35.6	25.6	11.1	

17 Least significant differences at 1 percent level, among individual species and treatment—26.7 percent; among treatments means—15.4 percent; among species means—13.4 percent.

The survival in October 1934 of the 20 jack pines planted in the spring of 1933 on weeded and control quadrats of each plot was:

Plot 37 weeded—16 plants; control—17 plants
Plot 38 weeded—19 plants; control—19 plants
Plot 39 weeded—17 plants; control— 9 plants

Heaviest mortality in this case was associated with severe rabbit browsing, recovery from which was slow in heavy shade. Of the 26 jack pine remaining on weeded quadrats following sampling in 1934, only one had died by 1938, whereas of the 21 remaining on control quadrats, six had died.

A

B

C

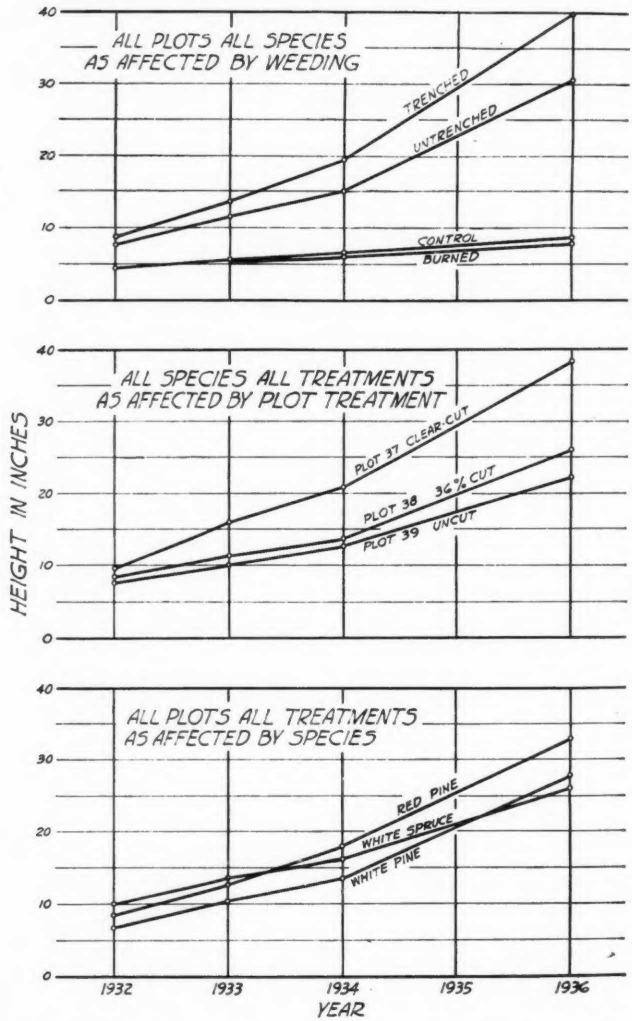


Fig. 10—Growth in height as influenced by A. by treatment of under vegetation, B. treatment of overstory, C. by species.

HEIGHT AND DRY WEIGHT OF TRANSPLANTS

Growth in height is shown in Figs. 10 and 11. Differences due to species and to treatment of quadrats and plots followed uniform trends throughout. Spruce, taller at time of transplanting but slower in growth, was eventually surpassed by both red and white pine in height. Jack pine in 100 percent light surpassed all others in growth rate, though being 4 years younger its height in 1936 was less than that of red pine.

Dry weights of transplants from trenched and untrenched quadrats followed trends similar to those for heights but differences were more striking, Fig. 12. White spruce maintained its position between the two pines throughout.

Height measurements made in 1932 and in 1936 were averaged for each species on each quadrat and analyzed by the variance method. At both times the differences between plots, species, and treatments and all first order interactions were significant at the 1 percent level. By the fall of 1934 dry weights of transplants varied from 1 gram on control quadrats to 339 grams on weeded quadrats in 100 percent light. To group control and weeded quadrats together by the analysis of variance method would serve only to obscure rather than to reveal differences; consequently standard errors for individual treatments were computed. Instead of a single error applying to all values the error increased with increase in dry weight.

Grouping the three species, red pine, white pine, and white spruce, together, the average heights and dry weights are as given in table 15. This table also shows the light intensity and available soil moisture during dry periods. Both

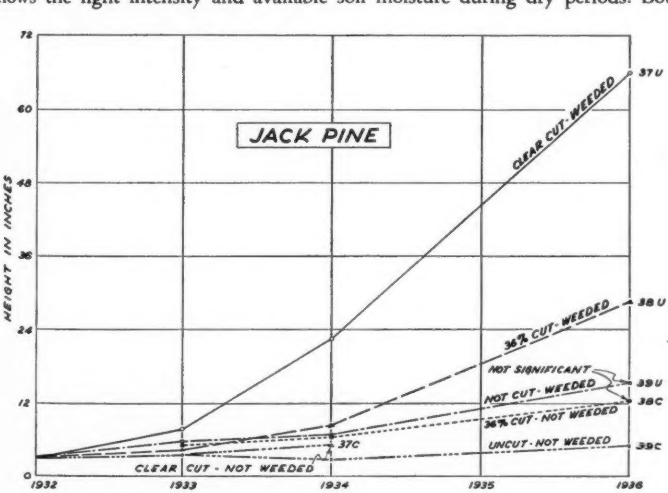


Fig. 11—Growth in height of jack pine as influenced by treatment of overstory and understory.

height and dry weight increased with increasing light intensity for the control, burned, untrenched and trenched series. Maximum dry weight and height occurred in full sunlight. Weight was more sensitive to treatments than height. A reduction in light from 100 to 21 percent reduced dry weight of trenched plants to 17 and of untrenched to 7 percent of their weight in full sunlight, whereas the corresponding heights were reduced to only 61 and 46 percent. Removing the root competition of the overstory without changing light intensity caused a significant increase in both height and dry weight. This increase was in each case accompanied by an increase in available soil moisture during dry periods which was probably responsible in part for the better growth. The severest competition was that caused by the undervegetation. No significant differences in either height or dry weight existed between transplants from burned and control quadrats. At 13 percent light intensity an increase in available soil moisture from 0.6 to 5.5 percent caused no significant change in either height or dry weight, indicating that adequate soil moisture can in no way compensate for inadequate light intensity. This statement is further substantiated by the fact that plants in 36 percent light but with only 2.6 percent

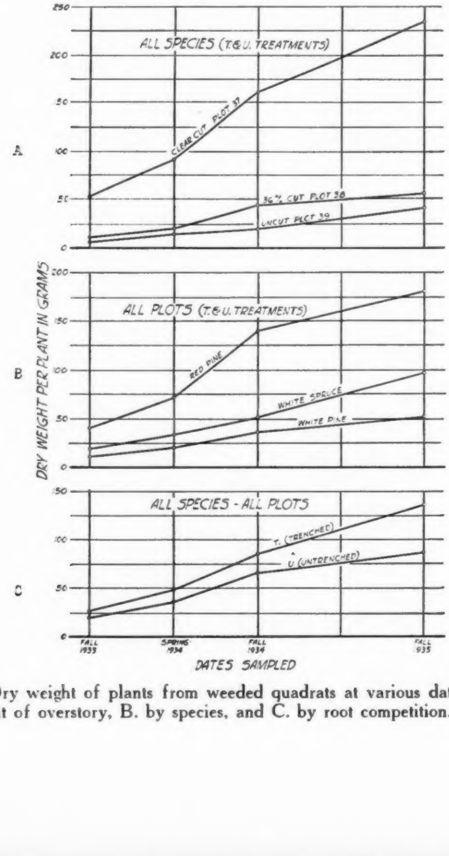


Fig. 12—Dry weight of plants from weeded quadrats at various dates as influenced by A. treatment of overstory, B. by species, and C. by root competition.

available soil moisture exceeded in dry weight all those grown in 23, 21, and 13 percent light even though in 5 of the 8 treatments at these intensities the available soil moisture was greater than 2.6 percent.

TABLE 15—Composite average height and dry weights of red pine, white pine, and white spruce transplants as influenced by light and root competition in an aspen forest.

Plot treatment	Quadrat treatment	Light intensity	Average available soil moisture during dry periods[18]	Height in 1936[19]	Dry weight in 1934	
					Mean	Standard error
		Percent	Percent	Inches	Grams	Grams
Uncut	Control	13	0.6	9	2	0.2
Clear-cut		13	5.5	10	3	0.7
36-percent cut		23	2.8	14	3	0.4
Uncut	Not Weeded Burned	13	0.6	9	2	0.3
Clear-cut		13	5.5	10	2	0.3
36-percent cut		23	2.8	12	3	0.3
Uncut	Weeded Untrenched	21	1.1	29	11	1.1
36-percent cut		36	2.6	29	36	10.8
Clear-cut		100	5.8	63	153	33.5
Uncut	Weeded Trenched	21	3.7	42	30	4.0
36-percent cut		36	4.3	49	54	6.5
Clear-cut		100	9.2	69	173	28.1

18 Available soil moisture = current moisture content – wilting percentage.
19 Least signficant mean difference at the 1 percent level 3 inches.

Both light intensity and soil moisture during dry periods were slightly more favorable on the control and burned quadrat of the partially cut plot than on untrenched quadrats of the plot that was uncut. In the case of seedlings that were grown in carefully spaded spots that eliminated root competition at the beginning, dry weight at the end of three years was the same with and without competition of under-vegetation provided light and moisture were essentially equal. The transplants, however, attained a weight of 11 grams with undergrowth removed and only 3 grams with it present. This suggests that factors other than light and soil moisture may be involved in the competition of the under-vegetation, a suggestion further substantiated by the fact that growth in 13 and 23 percent light in competition with the aspen and undergrowth was less satisfactory than in 11 and 20 percent light in the nursery where competition of other vegetation was excluded.[20] Moisture supply was adequate in both cases.

20 Recent unpublished studies by Schreiner at the Northeastern Forest Experiment Station furnish a clue to at least one such additional factor. He has found that roots of various grasses and weeds inhibit growth of hybrid poplars in field plantations. This inhibition also appears to occur even though the only source of contact is by means of a water culture solution that flows first through pots containing grass and second through pots containing poplars. Similar root antagonisms have been reported by other workers. Although not conspicuous among the subordinate vegetation grasses, notably *Danthonia spicata*, were present on all three plots.

TABLE 16.—Height and dry weights of transplants, as influenced by light intensity and root competition in an aspen stand.

Plot and quadrat treatment	Light intensity	Available soil moisture during dry period [21]	Height in 1936 [22]				Dry weight 1934 (fall) [23]			
			Red pine	White pine	White spruce	Jack [24] pine	Red pine	White pine	White spruce	Jack [24] pine
	Percent	Percent	Inches	Inches	Inches	Inches	Grams	Grams	Grams	Grams
Uncut — Not weeded										
Burned / Control	13	0.6	7	8	12	5	2	2	3	1
Clear-cut — Not weeded										
Burned / Control	13	5.5	8	9	15		2	1	4	1
36-percent cut — Not weeded										
Burned	23	2.8								
Control			11	13	13	12	3	2	3	1
Uncut — Weeded										
Untrenched	21	1.1	31	34	22	16	12	13	8	2
Trenched	21	3.7	37	40	22		36	28	25	
36-percent cut — Weeded										
Untrenched	36	2.6	34	32	21	29	65	20	23	4
Trenched	36	4.3	62	50	35		99	36	26	
Clear-cut — Weeded										
Untrenched	100	5.8	84	50	54	66	339	35	85	54
Trenched	100	9.2	83	61	62		289	89	141	

21 Available moisture = current moisture content minus wilting percentage.
22 Least significant difference 1 percent level 5 inches.
23 Least significant difference at 1 percent level varies by blocks from smallest to largest transplants as follows: 1, 3, 10, 32 and 153 grams.
24 Jack pine was 2 years younger from seed than the other species.

The heights and dry weights of individual species are shown in table 16. In this the plants from burned and control quadrats are grouped. The treatments are arranged in the order of increasing composite dry weight in order to bring out clearly the relationships between light and root competition on the one hand, and height and dry weight on the other. Light intensity shows a very close positive correlation with dry weight whereas available soil moisture during dry periods is only weakly correlated with weight. The respective correlation ratios are .99 and .75. Ratios of .80 or higher are significant at the .01 level.

After 4 years in the field, retardation of growth as expressed by the ratio between the lowest and highest weight, calculated from original data carried to the nearest centigram, was by species, red pine 1:199; white pine 1:77; white spruce 1:63. Jack pine, considering the fact that it was 4 years younger from seed, was retarded even more than red pine. White spruce shows up advantageously in this comparison by attaining greater height and dry weight than the other species in 13 percent light. This advantage in growth at low intensities is, however, so small that it has little practical significance; in 21 percent light with under-vegetation removed both red and white pine outgrew spruce. Measurements of height taken in 1938 showed that the trends exhibited in 1936 had continued. Jack pine had by this time surpassed all other species on both of the cut plots and though spindly, was second tallest on the uncut plot. Trees on control quadrats were exceedingly weak but more than twice the height of those outside the fence exposed to browsing.

STOCKINESS AND ROOT DEVELOPMENT OF TRANSPLANTS

The stockiness of the plants was calculated by determining the dry weight per unit length of top. The most striking and significant difference was that between weeded and unweeded quadrats which had average ratios of 9.0 and 5.0 respectively. The ratios were 7.2, 7.1, and 6.7 respectively for the clear-cut, 36-percent cut and uncut plots. Among the unweeded quadrats the highest ratios occurred on Plot 38. Other differences were slight or inconsistent and cannot be considered significant.

The stockiness of jack pine showed the same trend. The ratios were 23.4, 5.0, and 3.0 for weeded quadrats of clear-cut, 36-percent cut and uncut plots respectively, and for unweeded quadrats averaged 1.8 for the three plots.

A general impression of root development can be obtained from studying Fig. 13. When the plants were sampled both the top and root were measured, the root severed from the top and the two dried separately. It was found that the roots of the plants exhibited the same trends in dry weight as the tops, hence there is nothing to be gained by presenting the data separately. To determine whether root development were in proper proportion to top development the ratio between the two was obtained. The ratio of top to root was small for plants grown on the clear-cut plot, for those grown on control quadrats, and for white pine. The ratio decreased in the order trenched, untrenched, burned, and control. Two opposing influences operated in determining the ratio of tops to roots. Both high light intensity and dryness of soil tend to cause a low top-

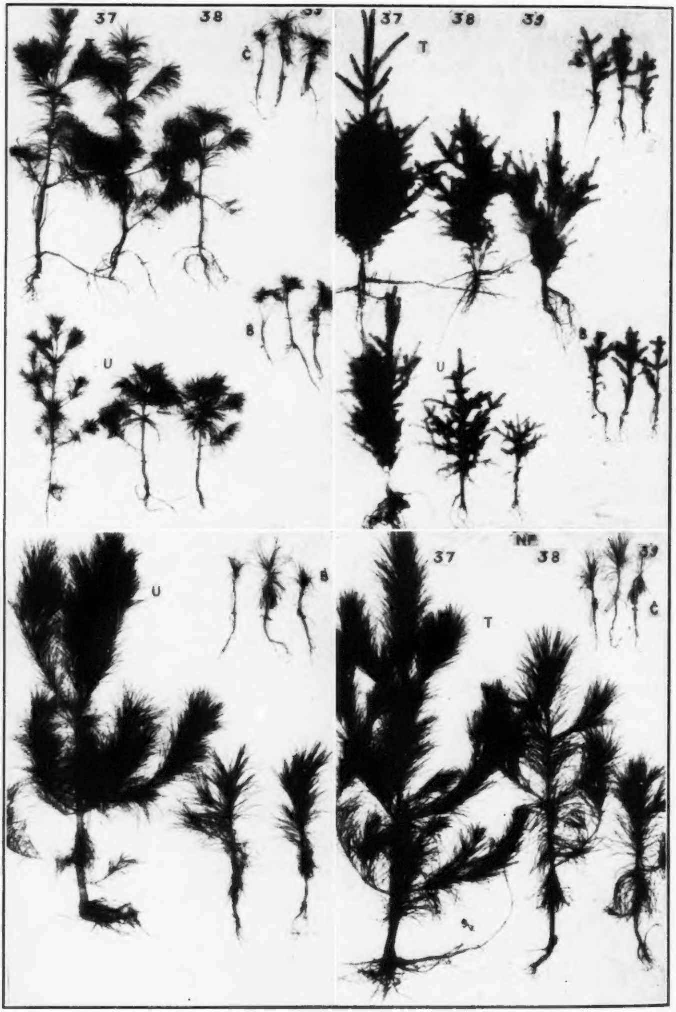


Fig. 13.—Photographs taken in 1934 of median plants showing influence of competition of aspen and of underbrush. Each group of 3 plants is arranged from left to right in the order: Plot 37, clearcut; Plot 38, 36 percent cut; Plot 39, uncut. The groups are designated as follows: T-trenched and weeded; U-untrenched and weeded; B-burned, not weeded; C-control, not weeded. The species are: upper left, white pine; upper right, white spruce; lower left and right, red pine. The scale on the right is 3.2 feet long and graduated in tenths.

root ratio (5, 16, 27, 29, 32). The plants in full sunlight had low ratios because of high light intensity and those from control quadrats because of low soil moisture. Here also differences in size of plants had a tendency to upset the effect of light and soil moisture on top-root ratio. The fact that top-root ratio decreased with increasing light intensity on the aspen plots, but showed no relation to light intensity in the nursery shades, may be explained in part by the fact that root development is more extensive in sand than in loam soils.

SUMMARY, ASPEN PLOTS

The direct effects of plot treatments, quadrat treatments, and species on the survival, growth and development of the conifers planted in aspen are summarized symbolically in table 17. Aside from survival of transplants, which was better on the shaded plots, clear-cutting was decidedly favorable. In other words, germination, first year seedling survival, height growth, dry weight of seedlings and transplants, and top-root ratio all responded favorably to increased light intensity. Survival of first year seedlings was in direct relation to seed weight. Among transplants, red pine gave poorest survival of all, largely because it was unable to compete with the under-vegetation; in growth it exceeded all other species except jack pine. It is an interesting and significant fact that among the species used, the relative rapidity of early growth was inversely correlated with ability to withstand intense competition whether measured by survival or by percentage retardation. Among quadrat treatments,

TABLE 17.—Summary of important differences [25] due to plots, species, and quadrat treatments.

Factor measured	Between plots [26]	Between species [27]	Between treatments [28]
Seedlings			
Germination	37, 39>38	S>W, R	U>T, C
Survival 1st season	37>38>39	W>R>S	U>T>C
Survival end of 3rd season	none significant	none significant	U, T>C
Dry weight	37>38>39	none significant	T>U>C
Transplants			
Survival	38, 39>37	S>W>R	T, U>C
Length of top	37>38>39	R>W>S	T>U>C
Dry weight of plants	37>38>39	R>S>W	T>U>C
Dry weight of top/ dry weight of root	38, 39>37	R>S>W	T, U>C
Dry weight of top/ length of top	none	none	T, U>C

[25] The symbol > means "is greater than." The comma connects two cases not significantly different; it should be read as "and."

[26] Code: 37—clear-cut plot; 38—36-percent cut; 39—uncut plot.

[27] Code: R—red pine; W—white pine; S—white spruce.

[28] Code: T—trenched and weeded; U—untrenched and weeded; C—control, not weeded.

germination, initial and final seedling survival were better on weeded quadrats. Survival of transplants, dry weight of seedlings and transplants, growth in height, root and shoot development were all best on trenched quadrats followed in order by untrenched and control. Burning the surface litter produced a temporary advantage which soon disappeared due to growth of the under-vegetation; it actually stimulated aspen suckers (34).

The entire study may be summarized by the statements:

1. Growth of all species increased, the more competition of other vegetation was removed.

2. The species which grew most rapidly when freed of all competition were least able to grow satisfactorily if competition was intense.

3. In the aspen forest competition of the under-vegetation was far more important in determining the success of coniferous seedlings than the shade or root competition of the trees in the overstory.

The behavior of the conifers under the more natural conditions of the aspen forest reflect in an intensified manner their behavior in the nursery shades. Because other factors were not always favorable 13 percent light was even more inadequate for survival than 11 percent light in the nursery. Growth increased with light intensity up to full sunlight as opposed to 43 percent light in the nursery. Using the same criterion of light requirements as in the nursery experiments, viz. reduction from the optima in survival and growth by low light intensities, the species increase in requirements as follows: white spruce, white pine, and red pine. Although covering a different time period, the data on jack pine would place it beyond red pine in light requirements. The further conclusions can be added here, first, that root competition tends to reduce growth irrespective of light intensity, but where light is below the optimum, removal of root competition can in no way compensate for inadequate light. The experiment does not provide a clear-cut expression of the relative importance of the two. However, at 21 percent light with root competition absent dry weight averaged 30 grams; at 23 percent light with root competition of both overstory and understory active dry weight averaged 3 grams. This is contrasted with an average dry weight of 163 grams in 100 percent light. In the nursery shades average dry weight in 11 percent light was 22 grams and in 43 percent light 128 grams. With light and root competition as they occur in aspen forests crown competition reduced growth by 80 percent and root competition by 90 percent of that attained by comparable plants free of one or the other forms of competition. Root competition of the overstory trees had an insignificant effect on survival, but root competition of the under-vegetation together with competition for light caused very high mortality. It may conceivably be argued that soil moisture and nutrients in the aspen forest were so favorable and aspen root competition so mild that the full potentialities of root competition in the Lake States is inadequately sampled by this experiment. To explore this argument we will now consider the results from a similarly designed experiment located on the dry sandy soils of a jack pine forest.

Establishment and Growth of Conifers as Influenced by Shade and Root Competition of Jack Pine

EXPERIMENTAL METHODS AND CONDITIONS

The desired degrees of contrast in jack pine canopies were available in a series of four one-acre plots cut over with their one-chain isolation strips by various methods in 1926. Records of growth of residual trees and of the establishment and growth of natural reproduction prior to and following cutting afforded additional information of value. The response of reproduction to cutting had been disappointing. New seedlings came in but most of them died out; at the end of five years there were no more present than before logging occurred. Here then was a definite case where reproduction was impeded due to unknown causes.

The stand was fifty-five years of age in 1926 and averaged 10,700 board feet per acre prior to logging. The cutting methods included light selection, heavy selection, and commercial selection which removed 20, 49, and 73 percent respectively of the basal area. A fourth plot remained as an uncut control.

The basal area and number of trees on the plots are shown by five-year periods in table 18. Natural red and jack pine seedlings, well established in 1930, grew during the course of the experiment in much the same manner as the planted trees; therefore, they served as an additional check on the experiment. Though natural seedlings caused an increase in the total stand on the

TABLE 18.—Stand remaining at different dates on jack pine experimental plots cutover in 1936.

Plot number	Basal area removed	Trees[29] per acre in			Basal area per acre in		
		1926	1931	1936	1926	1931	1936
	%	No.	No.	No.	Sq. ft.	Sq. ft.	Sq. ft.
9	0	348	322	332	128	135	141
10	20	273	279	343	91	99	106
11	49	208	201	342	63	67	77
12	73	109	99	305	24	19	22

29 Includes all trees 0.5 inch in diameter at $4\frac{1}{2}$ feet in height.

plots they had no effect on the experimental plants since they were neither large enough nor close enough to shade the planted conifers or to send their roots into the quadrats.

The more common native plants, at the time of planting, with their relative abundance on each of the plots, are listed in table 19. The under-vegetation was relatively rich in species, but the competition it afforded above ground was less intense than in the aspen stand. For the most part the vegetation was sparse with tall shrubs rarely forming a conspicuous secondary canopy such as

characterize aspen stands of the same age. Poverty oatgrass and other grasses were conspicuously dense on the more open portions of 49-percent cut plot. On the 73-percent cutting they formed a dense, very resistant sod. This sod was interrupted here and there by equally dense mats of low shrubs, mostly low-bush blueberry and bearberry. This type of ground cover was excluded from the aspen stand by the secondary canopy of tall shrubs.

Samples of soil, Cass Lake fine sand, from the four plots were surprisingly uniform, no one varying in any component by more than .7 percent from the mean. Soil fractions as determined by the Bouyoucos hydrometer method (6, 7) were: combined sand, 89.2 percent; conventional silt, 5.6 percent; conventional clay, 5.2 percent. The wilting coefficient was 2.6 percent. The site index was 65, well above the average for jack pine stands.

TABLE 19.—Relative abundance of various species in undervegetation of plots 9-12.

Species	Abundance by plots [30]			
	Uncut	20% cut	49% cut	73% cut
Trees				
Jack pine [31]	S	S	S	S
Red pine [31]	S	S	S	S
Pin cherry	S	S	S	S
Shrubs				
InlandJersey-tea	I	A	I	A
Dwarf bush-honeysuckle	S	S	S	S
Low-bush blueberry	A	A	I	I
American hazel	S	S	S	S
Beaked hazel	S	S	S	S
Bearberry	A	A	I	A
Ferns				
Bracken	I	I	A	I
Herbs				
Poverty oatgrass	I	A	A	A
Other grasses	I	A	A	A
Sedge	I	I	I	I
Mayflower	I	I	I	A
Northern bedstraw	I	I	I	I
Virginian strawberry	I	I	I	I
Wintergreen	A	I	I	A
Pearly everlasting	I	I	I	I

[30] Code: A = Abundant. Occupies more than 10 percent of area.
I = Intermediate. Occupies 1 to 10 percent of area.
S = Sparse. Occupies less than 1- percent of area.

[31] Reproduction.

Quadrats for planting were laid out corresponding to those used in the aspen experiment, but enlarged to 15 feet square, which proved to be a decided advantage because it allowed more choice in selection of planting holes. The surface sod and litter to a depth of about three inches was removed from trenched and untrenched quadrats to facilitate future weeding by means

of hoes. No live trees were included within any quadrat; stumps from trees cut five years earlier were included in a few instances. So far as practicable, trenched quadrats were checker-boarded with untrenched, and burned with control. Four quadrats of each type were laid out making a total of 16 on each plot. No fencing was done. The surface litter was burned with the brush burning torch as in the aspen plots. Areas to be seeded were prepared in the same manner as the quadrats to be planted, though the former were smaller in size.

Planting and sowing took place in October 1930. On each quadrat 25 two-year-old seedlings each of red pine, white pine, and white spruce, and 25 one-year-old jack pine were transplanted spaced 18 inches apart. Seedlings were rotated in each row as follows: red pine, white pine, jack pine, and white spruce, and arranged so that no two individuals of the same species stood side by side. Ten samples of ten seedlings each were chosen from the lots being planted to determine the initial dry weights. Jack pine seedlings had an average dry weight of 0.3 grams, the other three species 0.8 grams. The Chippewa planting iron which makes a large slit-shaped opening was used for planting. Losses among planted trees were replaced in the spring of 1931 but no replacements were made thereafter. Seeds were sown on mineral soil exposed by general scalping for trenched and untrenched areas, and by individual scalping on burned and untreated areas. Each spot was sown with approximately fifteen viable seed. Poisoned bait was systematically distributed over the area of each plot two weeks prior to sowing to eliminate seed-eating rodents; the effort, however, was unsuccessful. This first sowing resulted in very unsatisfactory seedling establishment; consequently all seedlings were removed and weighed in the spring of 1932. The scalped areas of trenched and untrenched treatments and the individual spots of burned and control treatments were then spaded to a depth of six inches, resown with fresh seed, carefully covered with fine soil, given a light dressing of aluminum sulphate and protected from rodents by conical wire screens. Excellent germination of red and jack pine resulted from the 1932 sowing.

The scalped quadrats were weeded periodically with garden hoes to maintain them free from competing vegetation. The plants were examined from time to time and notes taken on their general appearance and growth. Height measurements of all plants were taken each fall. The same procedure was followed in sampling plants and in handling samples as before. Plants collected in the field were packed in moist sphagnum and brought into the laboratory where they were washed, photographed, and weighed, then set aside for drying. The physical factors were measured in the same way as in the aspen plots.

The survival and growth of trees in this experiment was profoundly influenced by the ravages of May beetle larvae (*Phyllophaga* sp.) that caused heavy damage and loss to seedlings during the summers of 1933 and 1934. It was necessary to terminate the experiment earlier than had been planned because of damage from these insects. Trees two to three feet in height were attacked and killed on the heavily cut plots and on the scalped quadrats. Scalping removed organic material and the roots of other vegetation leaving only the roots of the planted trees for the larvae to feed upon. Here, during

the third and fourth seasons, these voracious insects destroyed the root systems of more than 80 percent of the trees.

Scalping had an additional disadvantage in probably significantly lowering the silt and clay content of the soil. The percentage of silt and clay in the upper two inches of mineral soil averaged 11.3 percent on the unscalped quadrats and 10.2 percent on the scalped, as determined by the Bouyoucos (6, 7) hydrometer method. Though a total of only thirteen samples were taken from each set, the odds that the difference is due to chance is 1 to 40. Browsing by deer and rabbits was rare and inconsequential on both weeded and unweeded quadrats.

THE PHYSICAL ENVIRONMENT

The light intensities for the 5-year period during which observations were made are given in table 20. As difference between weeded and unweeded quadrats was slight and not significant, a single value is given for each plot.

The temperature of the air, at the soil surface and at a soil depth of eight inches, increased regularly with increasing light intensity on both weeded and unweeded quadrats, table 21. A maximum difference of 9.5° C. existed between the surface soil temperature on trenched quadrats of plots uncut and 73-percent cut. This could account for no more than a 100-percent increase in dry weight in two years time. These differences are much larger than those found in the aspen stand, probably because of the greater dryness of the soil and because the soil was exposed by scalping. Temperatures high enough to be lethal to seedlings were not encountered on any of the plots on dates temperature was measured, though it is possible that they may have occurred on other dates (40). The entire site of this experiment was more exposed than that of the aspen plots. Records of weekly evaporation from paired Livingston spherical atmometers were kept throughout the growing seasons of 1931 and 1932. The weekly averages for the two-year period were:

Uncut plot ....125 cc.
20-percent cut plot ....120 cc.
49-percent cut plot ....143 cc.
73-percent cut plot ....136 cc.

TABLE 20.—Yearly average light intensity in jack pine plots.

Plot treatment	Light intensity					
	1930	1931	1932	1933	1934	Mean
	%	%	%	%	%	%
Uncut	27	26	24	18	22	23
20-percent cut	37	37	38	32	38	36
49-percent cut	51	46	56	48	58	52
73-percent cut	87	84	75	78	74	80

TABLE 21.—Temperature variations in jack pine plots.

Plot and quadrat treatment	Average deviation from daily mean[32] Air temperature	Soil temperature (surface)	Soil temperature 8″ depth
	°C.	°C.	°C.
Uncut	–1.5		
Weeded			
Trenched		–3.7	–1.2
Untrenched		–4.0	–1.5
Unweeded			
Burned and control		–4.0	–2.7
20-percent cut	–0.4		
Weeded			
Trenched		–1.8	– .3
Untrenched		–1.2	– .1
Unweeded			
Burned and control		–2.6	–2.0
49-percent cut	+0.4		
Weeded			
Trenched		+1.4	+1.5
Untrenched		+1.8	+1.3
Unweeded			
Burned and control		+1.2	– .7
73-percent cut	+1.5		
Weeded			
Trenched		+5.8	+2.9
Untrenched		+4.4	+2.5
Unweeded			
Burned and control		+2.7	+ .3

[32] Basis, records taken weekly throughout the four growing seasons from 1931 to 1934.

During the years 1933 and 1934 single determinations were made of relative humidity once weekly on each plot. These were averaged for each week and the deviations from the mean determined. These deviations averaged throughout the two-year period were:

Uncut plot	+0.2 percent
20-percent cut plot	+1.6 percent
49-percent cut plot	–0.1 percent
73-percent cut plot	–1.6 percent

Evaporation tended to increase and relative humidity to decrease with increasing light intensity similar to the increases in temperature. In fact the temperature difference is amply sufficient to account for the evaporation and humidity differences. The chief irregularity in this trend is caused by the higher evaporation and lower relative humidity on the uncut plot than on the

TABLE 22.—Available moisture content of soil during dry periods.

Plot and quadrat treatment	Available soil moisture 33												Mean
	1930			1932			1933			1934			
	July	Sept.		July	August		July			July	August		
	27	8	14	15	1	22	11	17	31	23	7	13	
		%			%			%			%		%
Uncut — Weeded													
Trenched	4.8	5.6	3.9	3.7	4.2	1.7	3.7	4.3	– .2	3.4	3.1	3.5	3.5
Untrenched	3.1	2.9	.4	....	.8	–1.2	2.0	– .4	–1.4	– .2	3.2	3.3	1.1
Not weeded													
Burned and Control	4.0	2.7	1.3	1.2	1.0	.7	1.4	.7	.2	3.7	1.9	1.9	1.7
20-percent cut — Weeded													
Trenched	3.9	6.0	6.0	4.7	4.6	4.4	4.6	1.1	1.7	3.3	– .3	3.1	3.6
Untrenched	3.0	3.8	2.2	– .9	1.8	–1.2	.9	.3	5.3	.9	.9	1.8	1.6
Not weeded													
Burned and Control	3.4	2.4	3.4	2.7	2.3	1.5	1.3	2.5	.5	1.0	1.8	2.2	2.1
49-percent cut — Weeded													
Trenched	2.0	3.5	2.9	2.8	2.7	2.4	3.3	.4	8.3	.1	.0	.9	2.4
Untrenched	2.7	2.2	.9	.2	2.1	– .6	1.2	1.6	4.9	.7	– .4	1.0	1.4
Not weeded													
Burned and Control	1.5	2.6	1.1	.8	1.3	5.5	2.7	.1	– .7	4.3	1.1	.1	1.7
73-percent cut — Weeded													
Trenched	1.7	1.6	3.2	2.3	2.1	1.8	3.3	–1.1	3.7	–1.3	–1.1	.3	1.4
Untrenched	1.1	2.4	3.3	– .2	.9	–1.0	– .2	– .5	.9	–1.7	–1.1	1.2	.4
Not weeded													
Burned and Control	0.8	.5	2.2	.7	– .2	–1.6	.5	.4	– .2	.8	.4	.3	.4

33 Available moisture = percentage soil moisture by weight-wilting percentage.

20-percent cut plot. This in turn is due to the nearness of the former to an open field which lies in the path of prevailing winds. The evaporation records are considered to be less reliable than those of relative humidity, because of the difficulties encountered in obtaining satisfactory performance of rain valves, and in keeping the evaporating surfaces free from algae.

Soil moisture samples were taken weekly throughout the four-year period in the same manner as in the aspen plots. The available soil moisture during dry periods is shown by plots and treatment in table 22. The soil moisture during dry periods averaged highest on trenched and lowest on untrenched quadrats of all plots. The moisture content fell to the wilting percentage or below six times on trenched, fourteen times on untrenched, and four times on control quadrats. It is concluded that scalping must have caused an increase in evaporation from the soil, as otherwise the moisture content on control quadrats which supported the most vegetation would have been lower than on untrenched quadrats. On all quadrats there was a slight increase in soil moisture on the 20-percent cut plot over that on the uncut plot which is consistent with the lower evaporation rate on the lightly cut plot. Critical soil moisture conditions occurred most frequently on 73-percent cut plot where there was little protective cover. This was true for all quadrat treatments.

ESTABLISHMENT, SURVIVAL AND GROWTH OF SEEDLINGS

The total germination for both 1930 and 1932 sowings, as expressed by number of spots bearing seedlings, was analyzed by the variance method to determine the effects of the various treatments on seedling establishment. Differences among plots, species, and sowings were significant at the 1 percent level. Differences among quadrat treatments were insignificant. Germination decreased regularly and significantly with increase in light intensity beyond 36 percent, table 23. Among species, jack pine germinated best followed in order by red pine, white spruce, and white pine. Three of the first order interactions were also significant. Significance of plot-species, table 23, is due to the fact that jack pine germinated almost equally well in 36 and 52 percent light, whereas the other species showed a marked decrease in germination at the

TABLE 23.—Germination by species and plot treatment.

Degree of cutting	Light intensity	Germination [34]				
		Red pine	White pine	Jack pine	White spruce	All species
%	%	%	%	%	%	%
0	23	78	70	99	94	85
20	36	90	71	90	76	82
49	52	66	40	91	58	64
73	80	49	11	60	9	32
	All plots	71	48	85	59	

34 Differences significant at the 1 percent level are: main effects, 9 percent; interactions, 19 percent.

higher light intensity. Significance of the quadrat-sowings interaction was due to the poor germination on the charred needle surface of burned quadrats in 1930. After eliminating the charred surface by spading in 1932, best germination occurred on these quadrats.

Data on survival at the end of the third growing season, of seedlings from the 1932 sowing, were analyzed by the variance method. Differences due to plots and to species were both significant at the 1 percent level. Inasmuch as losses were due chiefly to white grub activity, little importance is attached to these differences. Both grub attack and soil dryness were responsible for all seedlings dying in 80 percent light, whereas 37 percent survived in 23 percent light. Red pine and jack pine gave 25 and 39 percent survival as contrasted with 4 and 8 percent for white pine and white spruce. Differences of 10 percent are significant at the 1 percent level.

The surviving seedlings were lifted at the end of the third year and the average dry weight per seedling determined. The number of seedlings available was inadequate for statistical analysis. The average dry weights affected by plot treatment were:

Plot 9 (23 percent light)	.030 grams
Plot 10 (36 percent light)	.036 grams
Plot 11 (52 percent light)	.042 grams
Plot 12 (80 percent light)	.058 grams

by quadrat treatment were:

Trenched	.051 grams
Untrenched	.045 grams
Burned	.023 grams
Control	.039 grams

and by species were:

Red pine	.038 grams
White pine	.059 grams
Jack pine	.043 grams
White spruce	.014 grams

The increase in weight with increasing light, and the superiority of trenched and untrenched over burned and control treatments are clearly evident. Among species, the dry weights attained were in direct relation to the original size of seed with the single exception of jack pine which has a smaller seed than red pine.

Health and Survival of Transplants

The transplants on the uncut plot had thin stems and needles, symptoms of inadequate light intensity. These symptoms were also evident, though less pronounced, on the lightly cut plot. Best performance, all species considered, occurred in 52 percent light. On all plots transplants in weeded quadrats

appeared more vigorous than those on unweeded quadrats. Spruce, though making fair growth had chlorotic foliage in 80 percent light, probably a response to inadequate moisture and soil nutrients. Spruce appeared more vigorous in 23 and 36 percent light than on the other two plots. White pine was more vigorous than either red pine or jack pine in 23 and 36 percent light but was surpassed by jack pine in 52 and 80 percent light. Red pine was an indifferent performer on all plots compared with its excellent growth in the aspen plots and nursery cages.

Early differences in mortality of transplants were due largely to species and treatments, but those occurring in 1933 and 1934 were a reflection of the influence of species and treatment on the losses from root injuries caused by white grubs. In general, mortality increased with increasing light intensity (Fig. 14). The greatest losses occurred on the clear-cut plot and were due in part to the arid conditions prevailing there. Among species jack pine survived best, behavior consistent with its known superiority on sandy soils.

Weeding favored survival during the first three years but thereafter was harmful. This harmful effect was caused directly by white grubs that were obliged to concentrate their feeding on the conifer roots on weeded quadrats, whereas they were free to feed on roots of herbs and shrubs on unweeded quadrats and also on the flora supported by the duff and humus layers present.

The finding that losses due to drought were greatest on the heaviest cut plot where the soil was actually driest is consistent with observations on injuries and losses to natural vegetation on the same and similar areas caused by the severe drought of 1930 (37, P. 46). In both studies mortality was found to increase with decreasing density of the overstory.

HEIGHT AND DRY WEIGHT OF TRANSPLANTS

Growth in height on jack pine plots was far less rapid than that in the aspen stand. The total height at the end of four growing seasons even under the best conditions was but little over one foot for red pine, white pine, and white spruce, and slightly over two feet for jack pine. Even among transplants escaping grub attack height growth was considerably less rapid than in either the nursery or aspen plots. This is believed to be a reaction to inadequate soil moisture and nutrients on the jack pine site. Plants whose roots were injured by white grubs died or grew more slowly than those escaping attack. This caused a great variability in size and in number of plants available for growth records among and within unit treatments. Measurements of height taken later than the fall of 1933 or of dry weight taken later than the spring of 1933 were less complete or so highly variable that significance due to species, plot, and quadrat treatment was obscured. Height data for the fall of 1933 were analyzed by the variance method with corrections for disproportionality of subclasses (46). Actually this method of treatment is not strictly applicable because the number of plants available in the different treatments varied beyond the chi-square distribution. But inasmuch as the significance revealed is in agreement with that of analyses on height measurements taken at other dates not subject to this criticism, and since the trends are essentially uniform

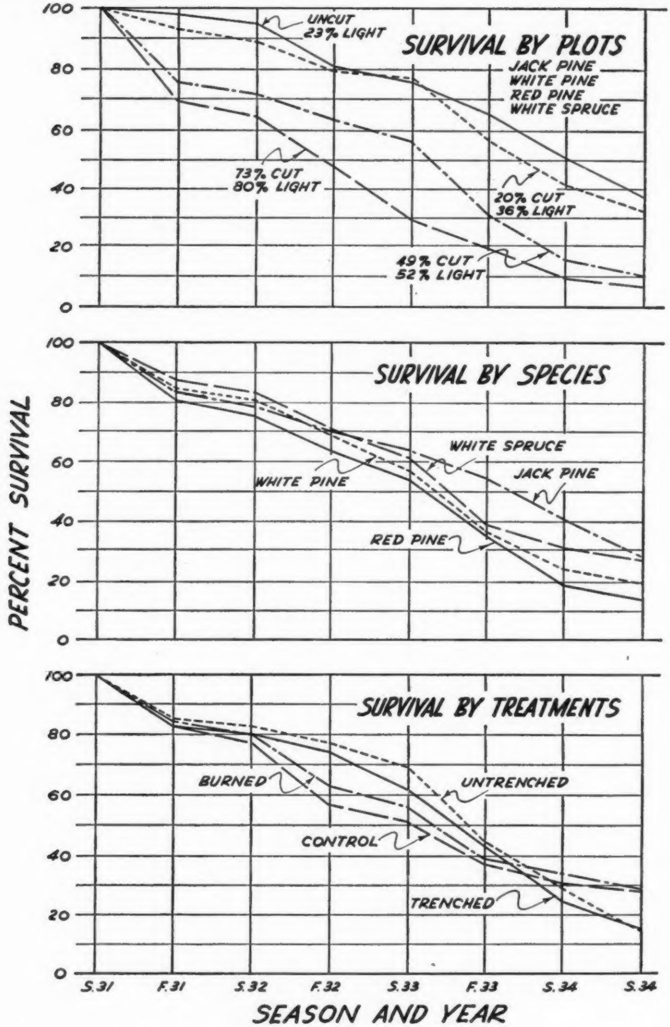


Fig. 14.—Survival of planted conifers as influenced by jack pine overstory, by species, and by competition of under-vegetation.

throughout, the writer feels justified in presenting this analysis. In the spring of 1933, two plants of each species were lifted from each quadrat on Plots 9 and 10 and one from each on Plots 11 and 12 for dry weight determinations. This gave a total in the first case of eight and in the second of four plants of each species from each plot and quadrat treatment. These data were analyzed by the variance method.

Both height and dry weight increased significantly with each increase in degree of cutting, table 24. Both also increased regularly with intensity of quadrat treatment, viz. control, burned, untrenched, trenched, though differences in dry weight of plants from burned and control quadrats were not significant. That surface burning in jack pine increased height growth and tended to increase dry weight increment of transplants, whereas in aspen it had no such effect, is due largely to the short interval from time of burning to time of measurement in jack pine that did not allow full recovery of the under-vegetation, and consequently of its competitive effect on the transplants. Among species jack pine was tallest and heaviest. White spruce was taller but not heavier than red and white pine.

TABLE 24.—Heights and dry weights of transplants in jack pine forest as affected by cutting of overstory, quadrat treatment, and species.

Source of variation	Average Height[35] Fall 1933	Average Dry Wt.[35] Spring 1933
	Inches	Grams
Plot treatment		
No. 9 — uncut; 23 percent light	10.5	3.3
No. 10 — 20-percent cut; 36 percent light	11.8	5.5
No. 11 → 49-percent cut; 52 percent light	15.3	7.7
No. 12 — 73-percent cut; 80 percent light	17.2	10.7
Quadrat treatments		
Trenched, weeded	15.1	9.8
Untrenched, weeded	13.0	7.1
Burned, not weeded	11.0	3.9
Control, not weeded	10.0	3.4
Species		
Red pine	9.4	5.4
White pine	9.5	4.9
Jack pine	17.2	8.7
White spruce	11.1	5.0

[35] Significant differences at 1 percent level, in height .8 inch; in dry weight 1.4 grams.

The influence of light intensity and competition of the under-vegetation on average height and dry weight for the four species is shown graphically in Fig. 15. Irrespective of the intensity of vegetative competition, dry weight increased with increasing light intensity up to 80 percent; height increased up to 52 percent on trenched quadrats and up to 80 percent on all others. Soil moisture during dry periods was greatest in 36 percent light and lowest in 80 percent light. Within any quadrat treatment, correlation between growth and soil moisture is completely masked by that due to light which clearly was the

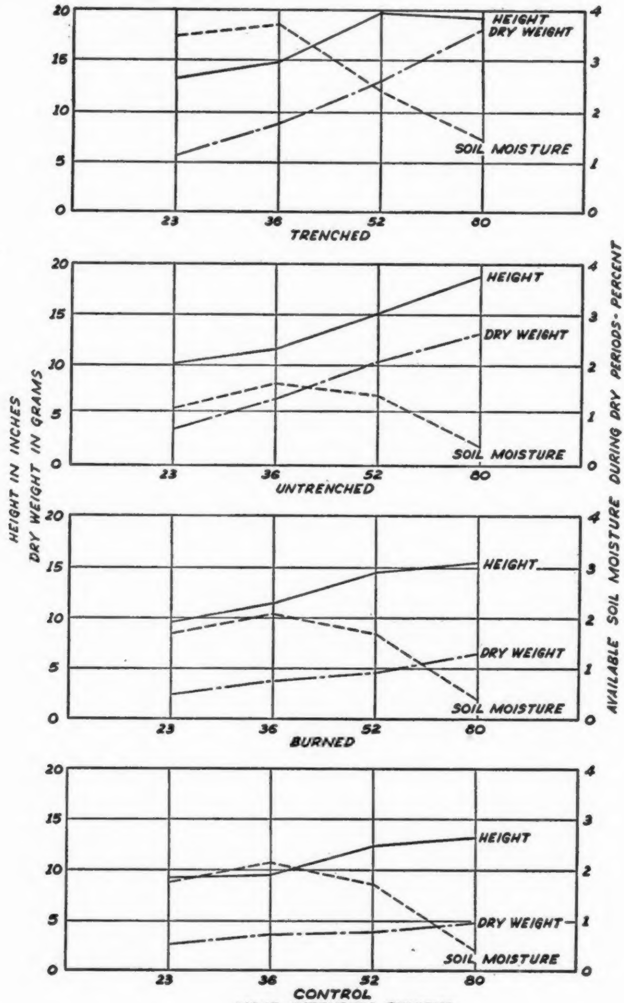


Fig. 15.—Height and dry weight of transplants from jack pine plots as influenced by light intensity and by quadrat treatments. Available soil moisture during dry periods is also shown for each treatment but is unrelated to growth.

dominant factor causing differential growth rate. It is only when height and dry weight of plants on trenched quadrats are compared with that on untrenched of the same plot that the effects of increased soil moisture on growth become evident. The excess in size of plants from the untrenched series over those from the burned and control series must be attributed to factors of competition other than light intensity or soil moisture (See footnote 20, page 567).

To bring out more clearly the influence of species, plot and quadrat treatment and their interactions on growth, the data are more completely displayed in table 25. Inasmuch as red pine differed significantly from white pine in height only on untrenched and burned quadrats in 80 percent light, and in dry weight only on trenched quadrats in 52 percent light, and since no significant differences between the two were due to plot or quadrat treatments, each taken as a whole, these two species are grouped together. Heights being the result of three years' growth and having been taken on more plants show more significant differences due to treatment than dry weights, though percentage differences of the latter are the greater.

Considering first the average heights and dry weights for the four species, it is seen that on each plot height and dry weight increased the more the competition of undergrowth and overstory were reduced. It is also significant to note that the response of dry weight to increased light intensity is the greater the more competition is reduced. Trenching in every case caused an increase in soil moisture above that of any other treatment. Weeding alone, however, tended to reduce soil moisture below that on burned and control quadrats, but nevertheless favored growth.

This table serves admirably to emphasize the fallacy of trying to stress the effect of root competition independent of light intensity. Root competition on trenched quadrats which varied only with size and density of transplants was least in 23 percent light and greatest in 80 percent light. This caused a corresponding decrease in available moisture during dry periods, but did not prevent dry weight from increasing with light intensity.

Root competition was unquestionably severe on all burned and control quadrats, yet here also dry weight increased with increased light intensity irrespective of soil moisture. On untrenched quadrats, where root competition of the overwood was progressively decreased with increasing light, the response of all species was pronounced.

The individual species follow the same trends in height and dry weight that their averages show. In height, which was greatest on trenched quadrats, white spruce attained the greatest values in 23 and 36 percent light, red and white pine in 36 percent light, and jack pine in 52 percent light. On the burned and control quadrats where competition was most keen, red pine, white pine, and white spruce showed little response in either height or dry weight to added light. Jack pine showed a significant response in all cases indicating that it is better able to cope with the competition of grass and low shrubs than the other species, provided the overwood does not cast a dense shade.

Perhaps the data can best be summed up by saying that where light inten-

TABLE 25.—Heights and dry weights of transplants as influenced by light and root competition in a jack pine forest.

Plot treatment	Quadrat treatment	Light intensity	Available soil moisture	Average height by species[36] Fall, 1933				Average dry wt. by species[36] Spring, 1933			
				Red & White pine	White spruce	Jack pine	All species	Red & White pine	White spruce	Jack pine	All species
		%	%	Inches	Inches	Inches	Inches	Grams	Grams	Grams	Grams
Uncut		23	1.7	7.5	9.6	11.7	9.1	1.7	3.9	2.5	2.4
20 percent cut		36	2.1	8.7	9.8	11.6	9.6	3.4	3.3	3.5	3.4
49 percent cut	Control	52	1.7	8.4	10.2	15.8	12.1	3.1	3.3	5.2	3.7
73 percent cut		80	0.4	9.7	12.5	16.9	13.2	3.3	3.7	9.4	5.0
Uncut		23	1.7	7.4	9.9	13.2	9.4	2.4	2.9	1.7	2.3
20 percent cut		36	2.1	9.6	11.0	14.4	11.1	3.4	4.7	3.7	3.8
49 percent cut	Burned	52	1.7	8.4	10.1	19.1	14.3	3.9	4.5	5.1	4.4
73 percent cut		80	0.4	8.3	11.7	18.9	15.3	4.9	6.4	10.0	6.6
Uncut		23	1.1	7.9	10.3	13.3	10.1	3.3	3.7	3.5	3.5
20 percent cut	Surface	36	1.6	9.4	10.3	15.7	11.7	6.2	4.4	8.4	6.3
49 percent cut	scalped	52	1.4	10.8	10.8	22.1	15.1	9.0	6.7	15.4	10.0
73 percent cut		80	0.4	10.9	12.2	20.9	18.8	11.9	8.2	20.9	13.2
Uncut		23	3.5	10.8	13.2	16.9	13.2	5.2	3.7	6.5	5.1
20 percent cut	Scalped	36	3.7	13.1	13.3	19.0	14.8	7.5	6.9	12.2	8.5
49 percent cut	and	52	2.4	11.2	12.8	24.0	19.6	10.8	8.7	21.4	12.9
73 percent cut	trenched	80	1.4	8.8	12.0	21.7	19.0	10.8	11.5	39.1	18.1

36 Least significant differences at 1 percent level:

	Red and white pine	Jack pine and white spruce	All species
in height (inches)	2.3	3.3	1.7
in dry weight (grams)	3.9	5.5	2.7

sity was low, 23 percent, response to weeding and burning was diminished; where root competition was severe, burned and control quadrats, response to increased light was diminished; and where either light intensity was low or root competition severe, difference in growth rate of species was diminished. These account for the significance of first and second order interactions.

At later dates after grubs had caused more damage, the same general trends persisted except that differences in height due to treatment diminished and differences in dry weight increased. Jack pine remained the tallest and heaviest; spruce was second in height but fourth in dry weight; and red pine exceeded white pine in both height and dry weight. Heights and dry weights increased regularly with increasing light intensity, and dry weights with increasing intensity of quadrat treatment. Difference in weight of transplants from trenched and untrenched quadrats increased, and from burned and control quadrats diminished with one additional growing season.

STOCKINESS AND ROOT DEVELOPMENT OF TRANSPLANTS

Stockiness of transplants grown in the shade of jack pine also showed a direct response to light intensity and other growth conditions as can easily be seen from Fig. 16. Ratios between length of top and dry weight of top were calculated for each transplant sampled in the spring of 1933 and the data analyzed by the variance method. Plots, quadrats, and species, and all first order interactions involving species were found to be responsible for significant differences. Stockiness decreased significantly with each decrease in light intensity and with decreasing intensity of quadrat treatment up to and including the burned ones. Jack pine was the most responsive of the four species to both plot and quadrat treatment and only it differed significantly from the others. It was far less stocky than the others in 36 and 23 percent light and on burned and control quadrats, but best of all in 80 percent light.

Root development, in so far as this could be determined in view of the severe injuries caused by white grubs, was in general accord with top development. The trees having the larger tops, that is those on the heavily cut plot, had also the larger roots. Ratios of root to top on a dry weight basis were calculated, but these showed relatively little change with either plot treatment or quadrat treatment except in so far as this was affected by grub attack.

SUMMARY, JACK PINE PLOTS

The main effects of differences in competition on the germination, establishment, growth, and development of conifers on jack pine plots are shown in table 26. Germination of seed and survival of seedlings and transplants was favored by overhead shade, the greater the shade, the better the germination and survival. Height, total dry matter, and stockiness increased with each increase in degree of cutting in the overstory. Among species, jack pine surpassed the others in germination, in seedling and transplant survival, and in height and dry weight of transplants. Of the four species, jack pine was most sensitive to competition showing greater variations in height, dry weight, and stockiness than the other species. Quadrat treatments had little effect on germina-

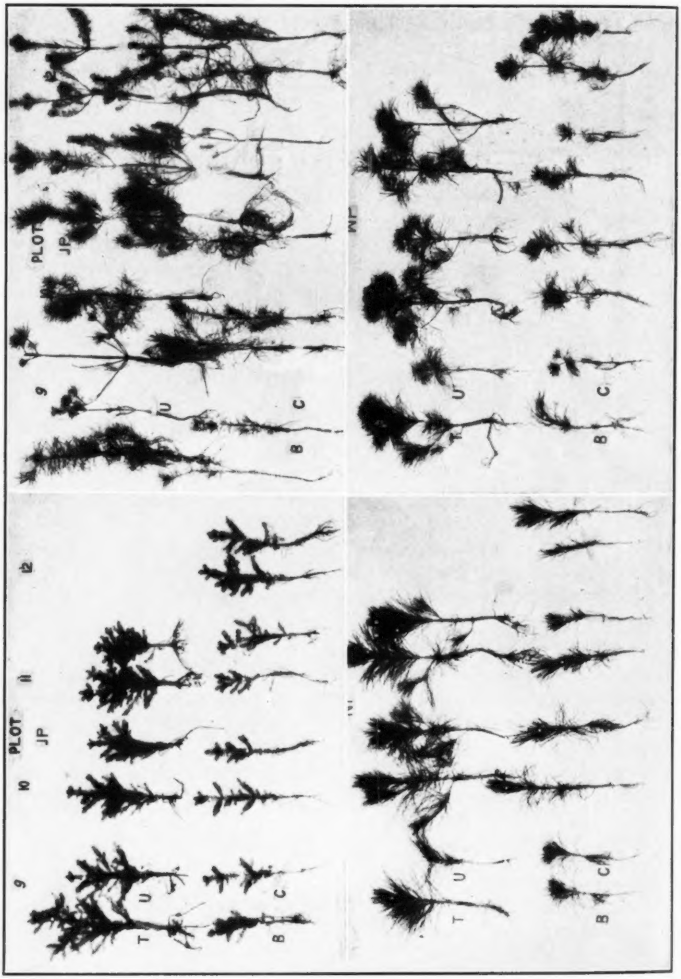


Fig. 16.—Photographs of median plants lifted in the fall of 1934. Plots 9, 10, 11, adn 12 had light intensities of 23, 36, 52, and 80 percent respectively. Upper left white spruce, upper right jack pine, lower left red pine and lower right white pine. Plants from each plot are arranged as follows: upper left plant from trenched quadrats, upper right from untrenched, lower left from burned, lower right from control.

tion, but profoundly influenced survival, growth, and development. Aside from the losses due to white grubs, which were greater on scalped quadrats, survival and growth were increased by removing the competition of the undervegetation and also that due to roots of trees forming the overstory. The major conclusions drawn from the nursery and aspen experiments are strengthened by the jack pine study. Growth in height and dry weight increased with light intensity up to 52 percent and 80 percent light respectively. Owing to the drier soil of the jack pine site germination and survival were improved by reduced light intensity even to a greater extent than in the aspen plots. Root competition at its greatest reduced growth by about 70 percent. This occurred in 80 and 52 percent light. In 23 percent light it reduced growth by only 53 percent. On trenched quadrats growth at 23 percent light was 72 percent of that at 80 percent light indicating under the conditions of this experiment about the same relative importance for the two types of competition. Based on growth, light requirements of the four species increase in the order white spruce, white pine, red pine, and jack pine. Both the aspen and jack pine experiments indicate that root competition involves more than competition for moisture; and also that the subordinate vegetation where dense is likely to be as serious if not a more serious source of root competition than the large trees. The further conclusion can be drawn here that of the four species, jack pine, which has the greatest light requirement is most able to withstand severe root competition and soil dryness. It alone was able to respond to added light when exposed to severe root competition.

TABLE 26.—Summary of important differences[37] due directly to species, plot treatment, and quadrat treatment among conifiers planted on jack pine plots.

Factor measured	Differences observed		
	Between plots[38]	Between species[39]	Between quadrats[40]
Among seed spots			
Germination	9, 10>11>12	J>R>S>W	none
First season's survival	none	none	T>U>B, C
Survival at end of 3rd season	9>11>10>12	J>R>S, W	none
Dry weight	12>11>10>9	W>J>R>S	T>U>B>C
Among transplants			
Survival	9, 10>11>12	J>W, S>R	U>T>B>C early B>C>T, U final
Height	12>11>10>9	J>S>W, R	T>U>B, C
Dry weight	12>11>10>9	J>R>S, W	T>U>B>C
Degree of stockiness	12>11>10>9	R, S, W>J	T>U>B, C

[37] The symbol (>) means "is greater than." This is used only where differences are statistically significant except for dry weight of seedlings. The comma connects two species or treatments not significantly different.

[38] Code:
- 9—uncut plot, 23% light.
- 10—20% cut, 36% light
- 11—49% cut, 52% light
- 12—73% cut, 80% light

[39] Code:
- R—red pine
- W—white pine
- J—jack pine
- S—white spruce

[40] Code:
- T—trenched, weeded
- U—untrenched, weeded
- B—burned, not weeded
- C—control, not weeded

If these three experiments have faithfully sampled conditions, we would expect to find our conclusions borne out by studies in extensive plantings and in natural stands. We would expect jack pine seedlings to be rare if not entirely absent beneath canopies transmitting only 12 percent light, and the other species, if present, to be in poor condition and growing very slowly. Where 20 to 35 percent light is available we should expect an abundance of conifer seedlings, other conditions being favorable, and high initial survival of plantations but growth again to be slow. Best growth would be expected in small openings where the plants receive full sunlight. Under uniform conditions of seedling establishment or in mixed plantings we would expect as light intensity decreased a decrease in abundance of all species first evident in jack pine followed in order by red pine, white pine, and white spruce. On the other hand, where root competition or dry soil are the major factors, we would expect jack pine to excel all others. White pine would be expected to excel on those sites where establishment is dependent on a large reserve food supply in the seed.

Extensive Studies of Conifer Reproduction in Relation to Light

The full significance of the intensive studies cannot be appreciated without knowing first what light intensity ranges occur in natural stands in which conifer reproduction is desired, and second, to what extent the behavior of the seedlings and transplants grown in the three experiments is typical of natural seedlings occurring on a variety of areas. These topics will be discussed for both aspen and pine stands.

Light Intensities and Conifer Seedlings in Aspen Forests

Light intensities were measured on thirty-one plots located in aspen stands varying in age from 20 to 50 years. Each plot was one-tenth acre in size. Light readings were taken at the 4-foot and 3-inch level at each of forty to fifty different stations, well distributed over the plot area. At the 4-foot level the light varied among plots from 11 to 40 percent with a mean of 23 percent and a median of 21 percent; near the ground surface it varied from 4 to 27 percent with a median of 9 percent. White pine and white spruce trees of seed-bearing age occurred irregularly throughout the stands in which the plots were located, and were actually present on six of them. Seedlings of white pine and white spruce, though sparse on all plots, were completely absent from only ten, of which eight had less than 15 percent light. Only one plot had an adequate stocking of seedlings, 1200 per acre, and it had 33 percent light.

Studies of establishment and growth of seeded and planted conifers and of naturally occurring pines and white spruce in competition with aspen and brush have been made on some eighty additional plots, which gave results as to range of light intensity and its influence on survival and growth in substantial agreement with those from Plots 37 to 39. Where both a brush cover and aspen overstory were present, light intensity was low, survival of conifers poor and growth negligible. On no plot did a single plant give promise of coming through the understory unaided. Removal of the understory by mow-

ing with a scythe without cutting the overstory improved both survival and growth rate, but not sufficiently to justify this as a practical procedure for converting aspen to conifers. On the other hand, cutting 80 to 90 percent of the aspen and all of the understory and keeping it cut back, preparing large sized scalped spots or furrows in which good quality stock was planted invariably resulted in high survival and growth comparable to that on weeded quadrat of clear-cut Plot 37. Conifer transplants could be brought through, though somewhat more slowly, by cutting the underbrush back only every other year. Grass sedge and other herbs not uncommonly invaded the scalped spots so that weeding with a hoe was required for best results, but it was found that herbaceous growth could be discouraged without serious harm to conifers by allowing a few tall shrubs to grow between the rows of planted trees. Data from some of these eighty-odd plots appear in summary form in a paper dealing with the conversion problem (43). Details on two sets of plots in which treatments were too conservative to be effective will be presented briefly. In 1926 four sample plots in 38-year-old aspen were established to determine the effect of various degrees of cutting on the establishment and growth of natural pine seedlings from surrounding seed trees, of seedlings of white pine and white spruce from seed sown in prepared spots, and finally of 3-year-old white spruce planted in 1930 on the plots. Seed spots were prepared as follows:

a. duff removed, spot screened
b. duff removed, spot not screened
c. duff undisturbed, spot screened
d. duff undisturbed, spot not screened

Germination and early survival were increased by screening and by removing the duff, but by 1930 all seedlings had died irrespective of spot or plot treatment. During the period 1926 to 1930 little change occurred in the number of natural white pine seedlings on each plot. Between 1930 and 1936 many seedlings died and a few new ones came in. The net change was a loss of from 33 to 82 percent. Growth was slow, averaging for all plots only 0.1 foot in height per year. The net loss and height by 1936 of both seedlings and transplants is shown in table 27. On part of each plot the underbrush was mowed once annually with a scythe from 1931 to 1935. This improved the survival and growth of spruce and also of a few white pines; but except for the clear-cut plot, where aspen sprouts as well as brush were cut, growth was slow. The low light intensity beneath the undergrowth was due in large part to shading by bracken and interrupted fern that were particularly dense on these plots. Practically all seedlings that were overtopped by the fern canopy succumbed within four or five years.

The second series consisted of six thinning plots established in 20-year-old aspen in 1929. Natural reproduction was sparse, hence each plot was seeded and underplanted to white pine and white spruce. Germination in seed spots from both spring and fall sowings was satisfactory but few seedlings survived the first summer and winter. By the third season, when dense undergrowth had reduced light on all plots to less than 10 percent, all seedlings had disappeared. Losses were heaviest during winter when the small seedlings became

buried beneath a mat of newly fallen leaves. Those escaping death from other causes eventually became buried and died. The planted trees being larger, 1 to 4 inches in height when planted, gave much higher survival. At the end of

TABLE 27.—Survival and growth between 1930 and 1936 of natural white pine and of planted white spruce as affected by aspen competition.

Degree of cutting[41]	Light intensity in 1930		Survival			Av. height per plant 1936		
				Spruce Transplants			Spruce Transplants	
	At 3 feet above ground	At 3 inches above ground	Natural white pine[42] seedlings	Undergrowth cut	Undergrowth left	Natural white pine seedlings	Undergrowth cut	Undergrowth left
Percent	Percent	Percent	Percent	Percent	Percent	Feet	Feet	Feet
0	12	4	18	76	53	.8	1.0	0.7
30	40	7	67	88	82	1.1	1.1	1.7
50	34	5	51	73	79	.9	1.1	1.0
100	35	6	43	61	36	1.9	1.3	0.5

41 Based on percent of crown area removed.
42 Based on difference between number alive in 1930 and 1936.

the sixth year, white pine varied in survival from 8 to 24 percent and in average height from 3.1 to 4.7 inches; white spruce varied in survival from 26 to 52 percent and in average height from 5.0 to 7.4 inches. Neither had averaged more than 1 inch per year in height growth.

LIGHT INTENSITIES AND CONIFER SEEDLINGS IN PINE FORESTS

From studies of 64 plots in red pine stands and 190 in jack pine, it was found that light intensity varied with both age and density of stocking. Light intensity in well stocked stands of red pine between 25 and 65 years of age is reduced to approximately 12 percent or lower. In 100-year-old stands it in-

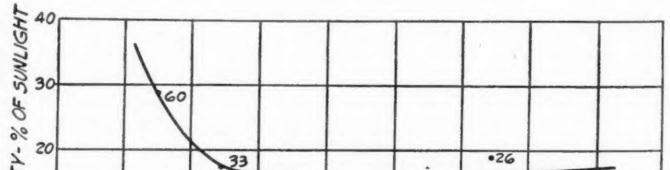


Fig. 17.—Light intensities in jack pine stands of different ages.

creases to about 15 percent and in 200-year-old ones to 40 percent or higher, table 28. The variation of light intensity with age of jack pine stands[43] is

TABLE 28.—Light intensity in red pine stands, by age of stand.

Age of stand [44]	Plots examined	Light intensity		
		Minimum	Maximum	Mean
Years	Number	Percent	Percent	Percent
25-35	9	3	18	7
55-65	1	..	..	11
90-110	10	7	26	16
200 and over	44	4	92	44

44 All stands were well stocked except those 200 and more years of age.

given in Fig. 17. Stands less than 20 years of age average 20 percent light or more, whereas those older than 20 years reduce the light to between 16 and 19 percent. As the young stands close and lower branches die, light progres-

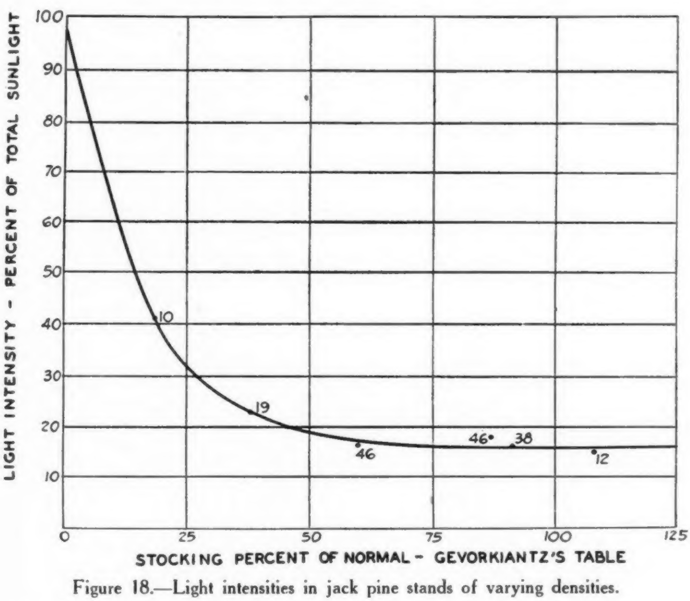


Figure 18.—Light intensities in jack pine stands of varying densities.

43 Studies of light intensity in relation to age and density of jack pine were made by R. W. Caird.

sively decreases until total live crown length approaches a maximum. Beyond this age the crowns require more and more room to sway in the breeze so that light intensity increases gradually until the stand begins to open up at maturity. Beyond this point light intensity is largely a function of stocking. It is interesting to note that little decrease in light occurs as stocking of jack pine increases above 50 percent (Fig. 18). This is apparently due to the fact that crowns are both longer and broader in understocked than in normal stands. It also furnishes evidence that approximately 16 percent light is necessary for needle survival on lower branches of jack pine, irrespective of stand density.

The occurrence and growth of pine seedlings in relation to light intensity in virgin red pine stands was studied in 1930 (35). Both density and growth rate of seedlings increased with increasing light up to at least 60 percent of full sunlight. Reproduction was usually adequate in amount wherever the light intensity was 20 percent or more, but satisfactory growth required 35 percent or more.

Further studies of the density of reproduction in relation to light intensity in red and white pine stands were made during the summer of 1931. A total of 28 plots was examined. Of the 16 plots having 15 percent light or less only 3 had as many as 400 seedlings per acre, whereas 9 of the 12 plots having 16 percent light or more were stocked with 400 or more seedlings per acre. Within the range 23-30 percent light, stocking was exceptionally good. One plot, however, deserves special mention. It was located in a stand of almost pure white pine growing on low ground not far from a swampy meadow. Although the light intensity was only 6 percent at the level occupied by pine reproduction there were a total of some 31,000 white pine seedlings per acre. When reexamined in the spring of 1938, it was found that the number of seedlings had greatly decreased. The original reproduction strips could not be relocated but nowhere were the seedlings as dense as 31,000 per acre. The most favored survivors had averaged less than 2.5 inches growth in height annually during the past seven years. A typical seedling, at least 12 years of age, is shown in Fig. 19. The behavior of seedlings on this plot serves only to emphasize the fact that though they become established in dense shade, mortality is high and growth almost negligible.

An experiment to test the effectiveness of trenching in a 200-year-old red pine stand was established in 1934. Four pairs each consisting of one trenched and one untrenched quadrat were laid out, on which all natural coniferous seedlings were charted and measured for height. The average height increment for two growing seasons was 2.7 inches on trenched and 1.9 inches on untrenched quadrats. The data were analyzed by the covariance method which showed the difference in increment to be significant at the 1 percent level after allowing for the regression of increment on original height. The average light intensity was 30 percent. The understory, made up of blueberry, bearberry, sedges, and grasses cast no shade on the natural pine seedlings. Slow growth was probably due in part to root competition of subordinate vegetation that was not disturbed in establishing the quadrats.

The natural pine reproduction was studied on 96 milacre quadrats established on each of plots 9-12 in 1926. This furnishes additional evidence of the

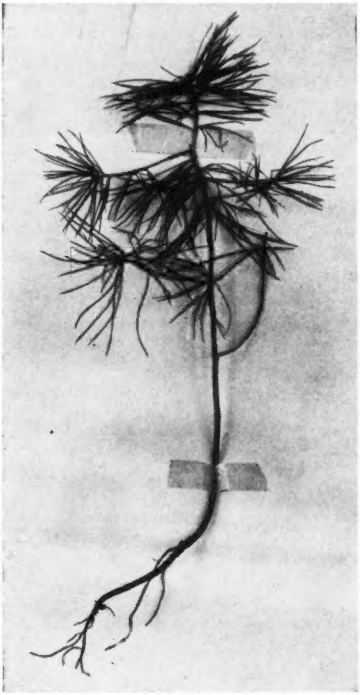


Fig. 19.—Dwarfed white pine tree 12 or more years of age and 10 inches in heighr. This seedling had been growing beneath a canopy which transmits only about 6 percent light intensity.

response of pine seedlings to light intensity. The changes in number of pine seedlings which occurred on each plot during the first 10 years after cutting are shown in table 29. On all plots the number of seedlings per acre varied from year to year, the losses being heavier following the severe droughts of 1930 and 1936. The losses, like those among conifers in planted quadrats, increased with increasing degree of cutting. Viewed from the standpoint of stocking, the reproduction appeared to be diminishing instead of increasing. This is probably due to the prevalence of droughts, increasing competition, and grub damage of recent years. The growth in height of the two largest seedlings on each quadrat on each plot was kept from 1932 to 1936. The average annual height increments by height classes and plots are shown in Fig. 20. The height increment increased with increasing degree of cutting up to 49 percent. Further cutting resulted in reduced height growth. This is in agreement with the performance of transplants with the exception that the latter attained greatest height on Plot 12.

TABLE 29.—Changes in natural pine reproduction during the first 10 years after cutting.

Plot treatment	Natural pine seedlings per acre					
	1926	1927	1928	1929	1931	1936
	No.	No.	No.	No.	No.	No.
Uncut	1260	1480	1420	1320	1020	960
20 percent cut	880	860	870	900	810	910
49 percent cut	890	650	560	960	850	890
73 percent cut	1080	1110	850	1480	680	460

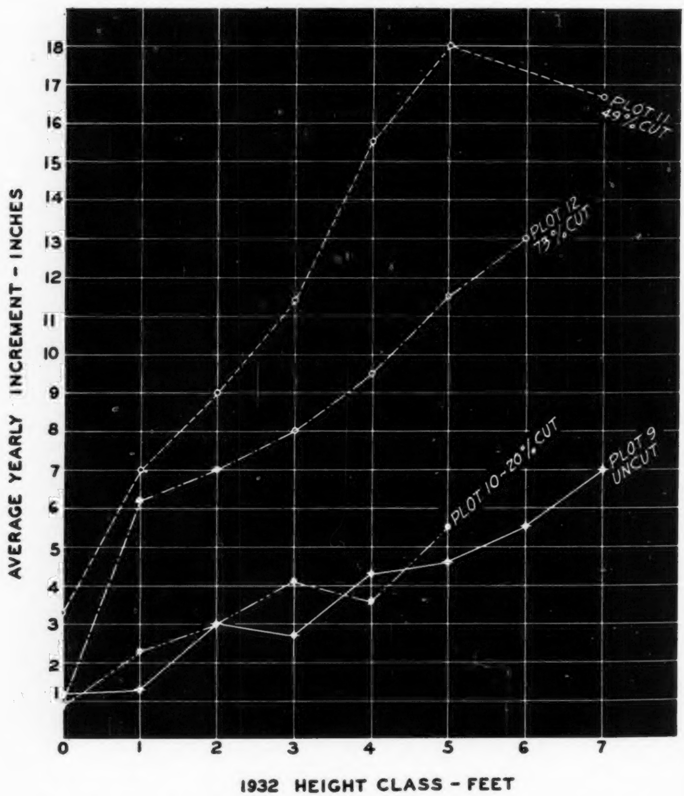


Fig. 20.—Growth in height of natural pine seedlings in response to cutting.

In 1934, 173 plots in jack pine stands 30 or more years of age were examined as to light intensity and abundance of pine seedlings. Due to the severe droughts of 1930, 1933, and 1934, reproduction was entirely lacking on 14 of the plots. Reproduction chiefly of red and jack pine was most frequent and abundant on plots having between 11 and 30 percent light. This further supports the finding that shade is favorable for the survival of pine seedlings. No data were obtained on the rate of growth of these seedlings.

Evidence from the extensive studies therefore corroborates that from the nursery experiment and from the intensive aspen and jack pine studies. Germination and initial survival is adequate in 20 percent light. Growth increases with light intensity up to at least 45 percent if root competition is absent, and up to at least 80 percent light with root competition present. White spruce survives better than white pine in the low light intensities encountered beneath secondary canopies in aspen stands. Red pine and jack pine are practically excluded from such stands if the under-vegetation is dense. Jack pine, on the other hand, excels all others on dry sites and where root competition is intense, but light intensity at least 50 percent.

Integration and Interpretation of Results

Certain major points of difference modified the results quite irrespective of experimental procedure. Chief among these was the soil. The aspen stands studied grew on fine sandy loam and loam soils that were much higher in moisture holding capacity, and judged by the vigor and growth of conifer seedlings in an experimental nursery located adjacent to Plot 37, were far more fertile than the fine sand soils in the nursery and on the various red and jack pine study plots. For this reason all species grew more rankly on clear-cut, weeded aspen land than in the nursery or on any of the pine plots. The fertile sandy loam soil made possible more complete utilization of available light intensity than the moderately fertile nursery soil or the poor soil in the jack pine forest. This finding is in agreement with studies of Gast (16 [p. 672-673]) and others (26 [p. 61-64] 27, 47) indicating that tree seedlings cannot attain maximum dry weight in high light intensity unless mineral nutrition is adequate.

Differences in growth due to treatments were greater in the aspen than in the nursery or jack pine plots, in part because a greater range in competition existed, and in part because the plants were given a longer period during which differential growth rates operated. Furthermore, the high light intensity in aspen stands together with the fertile soil made possible a luxuriant undergrowth of tall shrubs that were either absent or poorly developed in fully stocked jack and red pine stands. Where high shrubs were absent or poorly developed in aspen forests a rank stand of ferns, asters, and other herbs were common. Often these grew beneath the tall shrubs. Both shrubs and herbs cast a dense shade. The under-vegetation in jack pine, being composed mostly of low shrubs and herbs, casts little shade.

With these differences in mind it will be profitable to compare the results from the various study plots to bring out the effects of light and root competi-

tion on seedling establishment, survival and growth, and to review the meaning of tolerance as revealed by these findings.

GERMINATION AND SURVIVAL

In addition to the seed spots established on Plots 37 to 39 and 9 to 12, sowings were made in the nursery cages and on a large number of additional plots located in aspen, in jack pine, and in open areas. In all areas subject to surface soil drying, germination was improved by shading. Where the surface soil remained moist as it did in Plot 37, and in low areas seeded to conifers, little improvement in germination resulted from shade. Germination was somewhat more prompt at light intensities of about 50 percent than at 20 percent or less, but the difference in time of germination in no case was sufficiently great to be of any significance in subsequent growth and survival. Germination of all species was improved by sowing the seed in mineral soil and covering it to a depth of about one-eighth inch. The importance of mineral soil seedbed for germination of seeds of Lake States conifers has been emphasized in earlier papers (36, 42). Among quadrat treatments, trenching caused no increase in germination over that on untrenched quadrats. Burning the surface litter reduced germination if the seed were sown on the blackened soil, but had little effect where the surface was scalped to fresh mineral soil. The shade of the under-vegetation on burned and control quadrats had little influence on germination where an overstory remained, but was helpful on some of the experimental areas where the overstory was removed (42). Among the species used, jack pine and red pine germinated more promptly when sown in the spring, but gave no better results than white pine and white spruce when sown in the fall and protected from birds and seed-eating rodents over winter.

Survival of the seedlings during the first few weeks after germination was also increased by shading, though where damping off was prevalent, the shading proved harmful. The chief advantage of shade was in protecting the seedlings from drying of the surface soil and overheating of the surface which cause lesions near the ground line. Elimination of the under-vegetation improved first year survival in the aspen plots and, in fact, in a number of other aspen study plots where direct seeding was a part of the plan. In jack pine plots, under-vegetation was slow to invade scalped spots and therefore, had little effect on first year survival of seedlings. Initial survival in almost every case increased directly with increase in size of the seed. The white pine seed apparently contains enough reserve food to carry the seedling through the first summer, even though the light intensity is low. It also enables the seedling to send its roots through the humus layer into fresh mineral soil thereby more effectively evading droughts than the small seeded white spruce and jack pine. These, having little reserve food, are obliged to depend upon their own photosynthetic activity to survive the first summer. It is believed that reserve food in the seed is of considerable importance in enabling red and white pine seedlings to invade jack pine wherever their seed supply is adequate, and other vegetation absent.

First year survival of seedlings in 10 to 13 percent light was poor for all species in nursery cages, in the control quadrats of Plots 37 and 39, and on

the six aspen thinning plots. It was almost uniformly satisfactory in light intensities between 20 and 52 percent. This held true on both trenched and untrenched quadrats and even among control quadrats of the jack pine plots. At intensities of 80 percent and above, seedlings were exposed to surface soil drying and overheating which caused heavy losses especially in the sandy soils of the jack pine plots. It can be concluded, therefore, that germination and initial seed establishment is equally good in light intensities varying between 20 and 52 percent. First year survival is poor in light intensities of 13 percent or less, or of 80 percent or more.

Survival of seedlings beyond the first season and of transplants is dependent in aspen plots on their ability first to withstand winter temperatures and second to make sufficient growth to avoid smothering by leaves over winter. Winter killing was common in 11 percent light in the nursery and also in 13 percent light in the aspen experiments. Further evidence that low light intensities reduce resistance of plants to cold is presented by Dexter (11, 12) and Pearson (31). Lack of cold resistance in shaded tree seedlings is oftentimes obscured because smothering by leaves also occurs. Seedlings and transplants even five years of age or older may perish from this cause particularly where ferns are dense. White pine seedlings have an initial advantage over the others in this respect, but spruce because of its shorter needles and stiffer stem eventually surpassed it. Smothering of seedlings is less common in pine forests than in aspen and hardwoods. Both seedlings and transplants survived poorly in 13 percent light or less. This was true in the intensive aspen plots, the aspen thinning and other aspen plots, the red pine plots, and in the nursery cages where they were protected from leaves, rodents, insect damage, droughts, and other unfavorable factors. Survival was satisfactory in light intensities between 20 and 52 percent, with little difference showing up within this range. Survival was poorer in light intensities of 80 percent to 100 percent than in the intermediate range. This was apparently due to the inability of the plants to obtain adequate moisture to supply their transpiration requirements when exposed to high light intensities, since survival in the unshaded nursery beds was equally as good as in the light and lath shades at 46 and 43 percent light.

The removal of root competition of the aspen and jack pine trees caused no significant increase in survival, irrespective of the degree of overhead shade. This is particularly significant in view of the fact that three of the four years during which survival records were kept had moderate to severe droughts. Proponents of the root competition theory have claimed that the absence of tree seedlings beneath an overwood is caused by soil dryness due to root competition. In these studies, however intense the root competition of the overwood, its effect on survival was more than offset by the benefits of the shade, provided this did not reduce the light intensity below 20 percent. Even the very intense root competition of the under-vegetation of jack pine failed to cause important losses to transplants where they had the benefit of an overhead shade. The conclusion that during drought periods in the Lake States survival is increased by overhead shade corroborates the findings resulting from an extensive survey of losses following the 1930 drought (37). It seems safe to conclude, therefore, that root competition is not the direct cause of mortality

of coniferous species beneath aspen and jack pine canopies in the Lake States.

The finding that 13 percent light is inadequate for continued survival of conifer seedlings in natural stands in the Lake States is in sharp contrast to Burns' (9) report that white pine has a minimum light requirement of 5.8 percent of December 22 noon sunlight in Burlington, Vermont; to Bates' and Roeser's (4) that jack pine and red pine require 2.4 and 2.6 percent respectively for survival; and to Grasovsky's (18) that white pine requires 170-foot candles for survival and 340 for growth, approximately 2 and 4 percent respectively of summer sunlight on cloudless days. Burns' and Grasovsky's minimum requirements are the light intensity from a mazda lamp for the CO_2 given off in respiration of the leaves and stem to be balanced by that taken up in photosynthesis. Bates' and Roeser's requirements for survival are based on the light required from a mazda lamp burning 10 hours a day for seedlings grown from seed to survive for nine months and attain dry weight in excess of half the seed weight. Grasovsky's statement on growth is based on growth of three-year-old seedlings transplanted to pots and kept for 90 days in boxes illuminated by daylight from one end only. In his experiment growth was unquestionably at the expense of food reserve carried over from the nursery. In all three cases the plants were under laboratory conditions where all factors except light were favorable.

To survive under natural conditions the plants must not only produce sufficient food through photosynthetic activity to balance current respiration, but in addition they must build up a reserve to supply the roots, to offset respiration at night, and to keep them healthy over winter when temperatures are too low for active photosynthesis. In addition they must produce enough food to enable them to replace leaves, roots, and other tissue lost through senescence, and that lost through insect feeding, mechanical abrasion, and other vicissitudes of life on the forest floor. The finding that 13 percent light is inadequate and that 20 percent light is ample for survival is confirmed by the extensive survey of seedling occurrence in relation to light intensity in natural red pine and jack pine stands. It is also in agreement with Gast's (16) finding that at least 20 percent light is required for normal root development of Scotch pine, and Haig's (19) that western white pine planted in full shade actually lost weight and was unable to produce enough new roots to maintain necessary absorbing surface. Full shade in this case was approximately 4 percent sunlight for northern Idaho.

GROWTH

Maximum growth occurred in 43 and 46 percent light in the nursery and in 80 to 100 percent light in all aspen and jack pine plots where growth was studied in relation to light. The best index of growth is the accumulation of dry matter. The relative importance of light intensity and of root competition of overstories and undergrowth in the accumulation of dry weight of plants from the three separate experiments can best be reviewed by referring to table 30. For convenience, all species are grouped together and a single value given for each light intensity and each degree of root competition. Dry weights are

expressed on a relative basis, using the weight attained in the highest light intensity free of root competition as 100 percent. Plants from the nursery cages attained in 11 percent light, 18 percent of the dry weight they attained in full sunlight. Those in the aspen plots in the same light intensity but in root competition with both overstory and understory attained only 1 percent of the dry weight of those free of all competition. Plants from all three experiments freed of root competition showed an increase in dry weight with increasing light intensity up to 46 percent in the nursery cages and to 100 percent in the aspen and jack pine plots. With root competition of the overstory present, dry weight still increased with increased light intensity and in the case of aspen plots at a much higher rate than where root competition was eliminated. In jack pine plots, on the other hand, root competition made little difference in the degree of response to added light intensity. In other words, root competition caused the same proportionate decrease in growth at each light intensity. Where competition of both overstory and undergrowth were involved, growth was reduced to between one-half and one-third in the jack pine plots, and to one-eighth in the aspen plots of that occurring in the same light intensity without competition from roots.

The question has sometimes been raised, why do plants require light intensities of 50 to 100 percent of full sunlight for optimum growth, when only 1 percent or less of solar energy is actually stored up by photosynthetic process

TABLE 30.—Effect of artificial shade and root competition in aspen and jack pine stands on relative dry weight attained by conifers.

Root competition and habitat	Relative dry weight by light intensities, all species are grouped[45]				
	11-13 percent	20-23 percent	36 percent	43-52 percent	80-100 percent
	Percent	Percent	Percent	Percent	Percent
No outside root competitiion					
Nursery shades	18	42		109	100
Aspen transplants		16	31		100
Aspen seedlings		9	13		100
Jack pine		28	47	72	100
Root competition of overstory only					
Aspen transplants		6	21		88
Aspen seedlings		6	8		74
Jack pine		19	35	55	73
Root competition of overstory and understory. Burned and control grouped					
Aspen transplants	1	2			
Aspen seedlings	2	6			
Jack pine		13	20	22	32

45 The weights attained by conifers in the highest light intensity and freed of root competition form the basis for calculating percentages. Plants were grown for four years in the nursery cages and aspen plots, and for two years in the jack pine plots.

(39). The great portion of solar energy is consumed in heating the earth's surface, in evaporating moisture and other physical processes, and even though 20 to 30 percent of midday sunlight may be optimum for photosynthesis, 80 to 100 percent will be required in early morning and late afternoon hours. Furthermore even though upper leaves, exposed to full sunlight, have more light than they need, leaves of the lower and interior portions of the tree crowns are inadequately illuminated. The same applies to some extent to the individual leaf in that chloroplasts of inner pallisade and spongy parenchyma tissue where photosynthesis is most active often receive inadequate light for maximum photosynthesis. In any case, during the course of a growing season temperature, moisture and nutrient supply are likely many times to be inadequate in natural plant habitats for maximum utilization of solar energy.

Considering the results of all experiments, the question arises to what extent do the four species differ in physiologic requirements. At very low light intensities white spruce surpassed all others in survival, white pine surpassed red pine, and red pine, jack pine. This conclusion is based on all studies reported. The poor performance of white pine in the nursery, which may have resulted from poor stock or other causes, is overbalanced by its surpassing red pine in survival in 13 and 23 percent light in the aspen plots, and also by its seedlings occurring more commonly than those of red pine beneath red pine canopies transmitting 15 percent light or less. Differences among species in growth rate were small at light intensities of 13 percent or less; but at and above 20 percent light jack pine was clearly the fastest grower, followed in turn by red pine, white pine, and white spruce. The higher the light intensity, and the more favorable other growth factors, the greater were the differences among species. At no light intensity did spruce surpass red pine or jack pine in growth rate unless the intensity was so low that the latter species died, and in these intensities spruce was barely able to exist making little growth beyond that essential for mere survival.

Drought susceptibility, moisture requirements, and nutrient requirements were investigated concurrently in independent studies by the writer (37, 40, 44) and others[46] at the Lake States Forest Experiment Station. These showed that drought resistance increased and nutrient requirements decreased in the order, white spruce, white pine, red pine, jack pine.

THE MEANING OF TOLERANCE

Originally the term "tolerance" was used by foresters and ecologists to signify the capacity of tree seedlings and other plants to become established and live beneath a forest canopy and was thought of as tolerance of shade. This is still the generally accepted usage of the word, but during the 1920's considerable controversy arose as to whether this capacity depends on reaction to a single factor, tolerance of shade, or reaction to a complex of factors including tolerance of low temperature, low soil moisture, and low nutrient supply. Toumey (49 [p. 56]) states the case for the latter viewpoint as follow: "Tolerance should not be defined as the capacity of a tree to bear

[46] By Paul O. Rudolf and J. K. Stoeckeler.

shade, nor as a measure of light requirement, so long as we measure this capacity by the survival of the various species under different densities of natural canopies. Survival, under natural canopies, is dependent upon a complex of factors of which light intensity is but one, and often of subordinate importance.

"Tolerance should be defined as the capacity of a species or variety for survival, growth and development under natural canopies of varying degrees of density. It should be recognized that this is only in part a light relation." This definition was changed by Toumey and Korstian (51 [p. 332]) to: ". . . the ability of a tree to develop and grow in the shade of, and in competition with, other trees. In short, it is the ability of a tree to withstand competition and still maintain its growth." This definition is reaffirmed by Korstian and Coile (23). Without a statement describing what is meant by "maintain its growth" the definition is incomplete. The experiments reported herein, together with many others show definitely that all species investigated regardless of their relative tolerance undergo a marked reduction in rate of growth when light, moisture, or nutrient supply become inadequate as a result of competition. A more satisfactory discussion of the concept of tolerance is given by Baker (3) though his conclusion: "Real tolerance can be taken for all practical purposes as the tolerance a tree shows toward light (shade?) under average growing conditions—without attempting to define 'average'," will scarcely satisfy the exacting student of the question. He points out that the tolerant trees appear to have three adaptations for growing beneath an overstory:

1. Efficient photosynthesis at low temperatures and low light intensities.
2. Efficiency in use of water and nutrients under conditions of extreme competition.
3. A low level of metabolic activity.

He also points out, however, that attempts to link tolerance with water or nutrient supplies have not yet been satisfactorily substantiated by experiments. It is evident that none of these authorities feels that tolerance is a single factor relationship, but rather a composite relationship in which light, soil moisture, nutrient supply, and other factors of competition are involved. They also imply in their discussion that the several factors of competition react in a parallel manner on the establishment, survival, and growth of the several species.

The inconsistencies that arise from treating tolerance as a complex reaction to many factors are clearly revealed by comparing the relative reaction of the four species to shade with their reaction to such other factors as drought, nutrient supplies and heat, table 31. If tolerance were dependent on ability to withstand severe root competition for moisture or nutrients, then jack pine would be most tolerant and white spruce least tolerant. The same order would prevail if tolerance were dependent on juvenile growth rate in low or high light intensities or following release from suppression. This is the exact opposite to the order of tolerance as usually conceived. It is only natural that jack

pine, the pioneer species, should have lower moisture and nutrient requirements than red pine, white pine, and white spruce that follow it as plant succession progresses. They are able to do this not because of greater resistance to heat, heat injuries, drought, or nutrient deficiencies, but because they can survive longer at low light intensity. *Shade tolerance,* therefore, should be

TABLE 31.—The relative shade tolerance in comparison with other reactions of jack pine, red pine, white pine, and white spruce.

Reaction	Order of performance by species [47]			
	Jack pine	Red pine	White pine	White spruce
Tolerance of shade	4	3	2	1
Nearest in succession to the climax	4	3	2	1
Survival at low light intensities	4	3	2	1
Juvenile growth rate in 11 to 100 percent light intensity	1	2	3	4
Rate of growth following release from suppression [48]	1	2	3	4
Vigor in soil deficient in nitrogen [49]	1	2	3	4
Vigor in soil deficient in phosphorous [49]	1	2	3	4
Resistance to drought (56)	1	2	3	4
Establishment and survival of first-year seedlings	3	2	1	4
Root penetration of first-year seedlings	2	3	1	4
Resistance to heat (40)	No important difference			
Recovery from heat injuries (40)	3	4	1	2

47 The best performer is rated 1, the poorest 4.

48 Data from permanent sample plots 1 to 4, Chippewa National Forest.

49 Observations made during studies of influence of nutrients on drought resistance.

defined as *the capacity of a species to remain alive for long periods in low light intensity.* To avoid confusion it should always be qualified as shade tolerance. This definition neither involves nor implies anything as to drought resistance and nutrient requirements, or efficiency in the use of water and nutrients under extreme conditions; such evidence as was revealed by these and other experiments indicates that moisture and nutrient requirements are unrelated to the ability to live beneath dense forest canopies. This conclusion is further substantiated by the work of Mitchell and Chandler (28), who found that red, white, and chestnut oaks, trembling aspen, and red maple have low nitrogen requirements; pignut hickory, sugar maple, beech, and black gum, medium requirements; and white ash, yellowpoplar, and basswood, high requirements. No useful relationship between tolerance of low soil nitrogen and tolerance of shade can be drawn from this grouping. The definition also involves nothing as to a tree's ability to develop and outgrow other trees in dense shade or the efficiency of a tree's photosynthesis at low temperatures and low light intensities.

Many shade tolerant species exceed shade intolerant species in a number of adaptations that aid them in making the most of low light intensity. Among these are the capacity in low light intensity to increase height growth at the

expense of diameter growth, top growth at the expense of root growth, leaf area at the expense of leaf thickness, chlorophyll concentration at the expense of supporting leaf tissue, and light absorption at the expense of bloom, or other devices protective against water loss. None of these traits alone, however, can serve as a reliable index of shade tolerance. Also while these traits favor survival in low light intensity they lower resistance to deficient soil moisture. The proposed definition of shade tolerance therefore is based solely on the ability to survive for long periods at a low light intensity. This implies a low level of metabolic activity. This trait can readily be determined by cultivating plants in low light intensity and by observing survival beneath natural canopies that transmit less than 10 percent light. Confounding shade tolerance with drought resistance and nutrient requirements can readily be avoided; otherwise confusion results. Symptoms of inadequate light can be recognized without difficulty as can also symptoms of inadequate nitrogen, phosphate, or moisture. By recognizing individual causal factors silviculture can be placed on a much firmer basis. The writer contends, therefore, that our concepts of tolerance can be clarified only by differentiating between tolerance of shade, tolerance of drought, tolerance of low nitrogen, low phosphorus, low calcium, etc., and by using a qualifying term in discussing each of these.

Applications to Silvicultural Practice

The results of detailed studies of light requirements, drought resistance, and root competition do not provide an overall formula for handling forest stands nor are they expected to do so. Instead the object is to disclose information on fundamental biologic requirements that will provide the basis for a more intelligent approach to a wide range of silvicultural problems. Due to long familiarity with the experiments discussed and with extensive demonstrations based on their results, the major findings have already been incorporated into Lake States forest practice. Some of the results together with other material form the basis for a bulletin on conversion of aspen to conifers (43). The experimental results have been used directly or indirectly in papers on management of jack pine (57) direct seeding in the Lake States (42), and various mimeographed instructions issued by the Forest Service Region 9 office on soil preparation for planting, care of plantations, timber stand improvement, and harvest cuttings in pine, upland spruce, and aspen. To discuss these in detail would be out of place in this paper. A few of the more direct implications, however, will be mentioned.

Composition of future stands can be controlled through manipulation of crown density only under very intensive management. Assuming all species had become established, a dense canopy theoretically could be maintained until undesired species, say jack pine, had died, then the stand could be opened up to allow growth of the remainder. Actually this would be difficult to carry out because before all jack pine had died many red and white pines also would have died or be so slow in recovering from suppression that new jack pine seedlings might overtake them. Instead it is recommended that attempts to secure reproduction in conifer stands be deferred until near the end of the

rotation, meanwhile managing the overwood for maximum growth. This will usually prevent the development of a dense growth of shrubs or herbs, the presence of which incidentally is proof that the overstory is not completely utilizing the growing potentialities of the site. As the stand approaches final rotation age cuttings to favor reproduction are in order, but these should be timed to coincide with a good seed year if the stand is red and white pine and be preceded by proper seedbed preparation where seedlings are not already present. Following good seedling establishment, cutting to admit at least 50 percent light should be made.

Probably the most significant practical result of this study was to concentrate foresters' attention on the shrubs and herbs in the understory. The importance of the subordinate vegetation in the silviculture of the Lake States can scarcely be overemphasized. The results of cutting in conifer stands cannot be predicted accurately without an understanding of how cutting influences the high shrubs, low shrubs and herbs which are almost always present in all mature stands. Likewise the success of plantations depends in no small measure upon the protection afforded by, and competition provided by, subordinate vegetation. Competition of subordinate vegetation has been found to play a dominant role in determining the success of red spruce reproduction in the southern Appalachians (22) and in the Northeast (54) as well as of pine and white spruce reproduction in the Lake States.

Summary

Surveys of light intensity were made in stands of aspen, red pine, and jack pine on the Chippewa National Forest. Light above the undergrowth averages in fully stocked stands of aspen, about 23 percent; in 50- to 60-year-old jack pine, 15 percent; in red pine 55- to 65-years-old, 11 percent; 90- to 110-years-old, 16 percent; and in 200-year-old stands, 44 percent.

Experiments in artificial shading in a nursery indicate that at least 20 percent light is necessary for satisfactory establishment and growth of seedlings of red pine, white pine, jack pine, and white spruce. Equally high survival occurred in 43, 46, and 98 percent light. Maximum height growth occurred in 43 or 46 percent light. White pine and jack pine attained maximum dry weight in 43 and 46 percent light respectively, red pine and white spruce in 98 percent light. In 11 percent light jack pine differed but little in dry weight from white spruce and red pine; in all other light intensities jack pine was two or three times as heavy as red pine. In 43, 46, and 98 percent light red pine was twice as heavy as white spruce. It also exceeded white spruce in weight in 11 and 20 percent light. White spruce exceeded white pine in weight under all light conditions. White pine made the slowest growth of all in the beginning; consequently it underwent suppression by the other species.

The growth of the same four species of conifers was studied in three aspen plots where they were exposed to different degrees of competition of the overstory and under-vegetation. The aspen on one plot was cut clean, on a second 36 percent of the basal area was removed, on the third the trees remained undisturbed. Conifers were seeded and planted in quadrats given the following

treatments: (a) trenched, all undergrowth removed two or more times annually, roots of older trees severed by trenching; (b) untrenched, all undergrowth removed two or more times annually, roots of older trees undisturbed; (c) burned, surface litter consumed by fire in late autumn, no further treatment; (d) control, undergrowth undisturbed throughout. Light intensities beneath the under-vegetation averaged 13 percent on the uncut and clear-cut plots, and 23 percent on the partially cut plot. Where the understory was removed the intensities averaged 21, 36, and 100 percent for the uncut, 36 percent cut and clear-cut plots respectively. Temperatures in the air, surface soil, and soil at 8 inches depth averaged from 1 to 3 degrees C. higher on the clear-cut plot and 1 degree lower on the uncut plot than on the partially cut plot. Trenching caused no significant change in average soil temperatures, but removal of the subordinate vegetation caused a distinct increase in temperature.

During dry periods soil moisture was higher on trenched than on the other quadrats. Germination, first year seedling survival, growth in height of transplants, dry weight of seedlings and transplants were all greater the greater the light intensity. Survival of transplants and subsequent survival of seedlings was better on shaded than on unshaded plots. Among species first year survival of seedlings increased with increasing seed weight. Jack pine and red pine transplants had very low survival where competition of the undergrowth was intense but high survival where the undergrowth was removed. Red pine grew faster than white pine or white spruce where competition of other vegetation was reduced by weeding and by cutting or trenching.

Among all species the greatest response in growth, as measured by total dry weight, followed removal of competition of the under-vegetation. Survival of transplants, dry weight of seedlings and transplants, growth in height, and root development were greatest on trenched, followed in order by untrenched, control and burned quadrats. Burning caused an increase in the competition of aspen suckers and probably in that of subordinate vegetation.

An experiment similar to the one in aspen was carried out in jack pine on four plots cut as follows: uncut, 20 percent cut, 49 percent cut, and 73 percent cut; the light intensities averaged 23, 36, 52, and 80 percent respectively. Quadrat treatments were the same as in aspen, but since the under-vegetation in jack pine was composed chiefly of low shrubs and herbs, the light intensities were little affected by the undergrowth. Surface soil temperatures were 6 to 9° C. higher on the 73 percent cutting than in the uncut plot, air temperatures were 3° C. higher. Soil moisture during dry periods was higher on trenched quadrats of all plots except that from which 73 percent of the stand had been removed. Here evaporation from the soil surface reduced the moisture content below that on burned and control quadrats.

Germination and survival of seedlings and transplants was better the greater the shade of the overstory. Height, dry weight, and stockiness increased with increasing light intensity. Among species jack pine had greater germination, survival, height and dry weight than the other three species. Of the four it also was the most sensitive to reduced light. Removal of the under-vegetation by scalping caused a pronounced increase in losses due to root injuries by

white grubs, but aside from this survival and growth was favored by trenching and by weeding.

The findings from the intensive experiments in the nursery shades, in aspen and in jack pine were tested by surveys made of light conditions and natural conifer reproduction in aspen, red pine, and jack pine stands. These surveys confirmed the finding that competition of the subordinate vegetation is one of the most important factors preventing invasion of aspen forests having a conifer seed supply. Satisfactory growth was found to depend upon reduction of competition by cutting the overstory and by weeding the understory. The possibilities of pine seedlings adequate to produce well stocked stands successfully invading established aspen forest within a reasonable period of time appear remote.

In red pine stands adequate pine reproduction was infrequent where the light intensity was less than 15 percent, but common where the intensity was more than 20 percent. Stocking was very satisfactory in 23 to 30 percent light. Growth, on the other hand, was found to increase with increasing light up to 60 percent intensity. Trenching in a mature red pine stand not accompanied by weeding of the understory resulted in a small but significant increase in the height growth of natural reproduction over that occurring on untrenched areas.

In jack pine stands, pine seedlings were most frequent and abundant in light intensities of 11 to 30 percent; growth in height on the other hand, was greatest in intensities of 52 percent or higher. Survival during the drought years between 1930 to 1936 was found to be low with 80 percent light or more, but equally good in 36 to 52 percent light.

In all types of stands studied the success of coniferous reproduction was dependent chiefly upon the absence of intense competition of the subordinate vegetation. Compared with this the shade and root competition of trees comprising the overstory were of secondary importance. Shade of the overstory, if not too dense, was found to favor both germination and survival of seedlings, particularly on the drier soils where root competition for moisture appears to be more keen.

Either shade or root competition may be limiting factors in the growth of young conifers. Shade is likely to be the more important under the secondary canopies in aspen stands; root competition the more important among low shrubs, grass and other herbs beneath red and jack pine stands.

Despite the occurrence of severe droughts during the course of the experiments, survival beneath aspen, red pine, and jack pine canopies was found to be dependent more on adequate light intensity than on the degree of root competition. The ability of the four species to survive in dense shade increases in the order: jack pine, red pine, white pine, and white spruce. This is independent of their drought resistance, nutrient requirements or relative growth rate in low light intensities. Tolerance may be defined as the capacity of a species to remain alive for long periods in low light intensities and should be qualified as shade tolerance. The results reported indicate that linking shade tolerance to either moisture or nutrient requirements is unnecessary and tends to destroy the usefulness of the concept.

These results are valuable to the forest manager in clarifying and sharpening the concept of tolerance, in focusing his attention on the importance of the under-vegetation, in pointing out the need for adequate light for growth of natural reproduction and planted trees, and in emphasizing the difficulties involved in controlling composition through manipulating crown density. Finally they serve to impress foresters with the facts that successful conversion of aspen to conifers and successful natural reproduction of pine and spruce forests require conscious effort to maintain favorable light and other conditions for growth.

APPENDIX

The common and scientific names [50] of trees, shrubs, and herbs mentioned in this article are as follows:

TREES

Common name	Scientific name
Balsam fir	*Abies balsamea*
Red maple	*Acer rubrum*
Paper birch	*Betula papyrifera*
Spanish cedar	*Cedrella odorata*
White ash	*Fraxinus Americana*
Walnut	*Juglans nigra*
Gum	*Liquid ambar styraciflua*
Yellow poplar	*Liriodendron tulipifera*
White spruce	*Picea glauca*
Sitka spruce	*Picea sitchensis*
Jack pine	*Pinus banksiana*
Shortleaf pine	*Pinus echinata*
Western white pine	*Pinus monticola*
Longleaf pine	*Pinus palustris*
Red pine	*Pinus resinosa*
Pitch pine	*Pinus rigida*
Northern white pine	*Pinus strobus*
Loblolly pine	*Pinus taeda*
Balsam poplar	*Populus balsamifera*
Bigtooth aspen	*Populus grandidentata*
Quaking aspen	*Populus tremuloides*
Pin cherry	*Prunus pennsylvanica*
Black cherry	*Prunus serotina*
Douglas-fir	*Pseudotsuga taxifolia*
Oak	*Quercus*
Bur oak	*Quercus macrocarpa*
Mahogany	*Swietenia mahagoni*
Teak	*Tectona grandis*
Hemlock	*Tsuga canadensis*
Western hemlock	*Tsuga heterophylla*

SHRUBS

Round-leaved shadblow	*Amelanchier sanguinea*
Pearl everlasting	*Anaphalis margaritacea*
Bear berry	*Arctostaphylos uva-ursi*
Inland Jersey-tea	*Ceanothus ovatus*
Round-leaved dogwood	*Cornus rugosa*

[50] Nomenclature follows Sudworth (48) for trees; American Joint Committee on Horticultural Nomenclature for shrubs and herbs (2); Hitchcock, A. S. (21) for grasses.

American hazel	*Corylus americana*
Beaked hazel	*Corylus rostrata*
Dwarf bush-honeysuckle	*Diervilla trifida*
Wintergreen	*Gaultheria procumbens*
Lowbush blueberry	*Vaccinium pennsylvanicum*

HERBS

Pteriodophytes

Interrupted fern	*Osmunda claytoniana*
Bracken	*Pteris aquilina*

Monocotyledons

Sedge	*Carex* spp.
Poverty oatgrass	*Danthonia spicata*
Grass	*Gramineae* spp.
Canada mayflower	*Maianthemum canadense*

Dicotyledons

Wild-sarsaparilla	*Aralia nudicaulis*
Bigleaf aster	*Aster macrophyllus*
Virginia strawberry	*Fragaria virginiana*
Northern bedstraw	*Galium boreale*

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The Genus Carex in Tennessee[1]

J. K. Underwood

The *Carex* flora of Tennessee is still imperfectly known, as shown by the additional material collected, which extended the ranges of some species. The total number of species now known to this State is larger than might be expected, even though Tennessee is favorably located geographically. With its western limits in the Mississippi valley, it has species coming in from the north and west. The south-central tier of counties especially Franklin and Coffee, have species characteristic of the coastal plain. The eastern highlands provide ideal conditions for species which are characteristically northern, and the cool, protected coves and ravines in these highlands harbor coastal plain species as well. A few species also are endemic to this area.

Some general notes on the soils and topography of the State will present a better picture. Because of the wide variations in geological formations, there are many soil types with remarkable differences in fertility. Poor land may lie adjacent to fertile land of different origin. The line of demarcation is often easy to distinguish. For example, it is frequently possible to stand with one foot on the heavy yellow-red soil derived from the Chickamauga limestone and the other foot on the reddish-brown loam whose origin is the Holston marble. And so it is throughout half the State.

The natural divisions of the State also vary greatly in elevation. East Tennessee is the most elevated, and includes the Smoky Mountains on its eastern border, which attain heights up to 6,600 feet; and the parallel ridges and valleys which make up the broad depression of the great valley of East Tennessee lying between the Smoky Mountains and the Cumberland Plateau. The Plateau, which rises to an average of about 1600 feet, is distinctly different from any other section in both soil and climate. The Plateau is from 30 to 50 miles wide, extending in a southwesterly direction from Kentucky to Alabama, the major portion of which is gently undulating. The depressions often are swampy, affording habitats for a great variety of moisture-loving plants. The Plateau is capped with sandstone, which is near the surface over much of the area. Deep gorges run off from the margins and afford fine areas for collecting plants. On the eastern edge of the Plateau, especially, there are miles of escarpment primarily in the lower portion of the range.

The Central Basin of Middle Tennessee is an undulating plain with an elevation of about 600 feet, but it embraces hills which not uncommonly rise 200 feet or more. This area is of limestone origin, and contains a large amount —about 40 per cent—of so-called "glady" land. The glady areas have very shallow soil, with the limestone outcroppings over large areas. Cedar grows here naturally.

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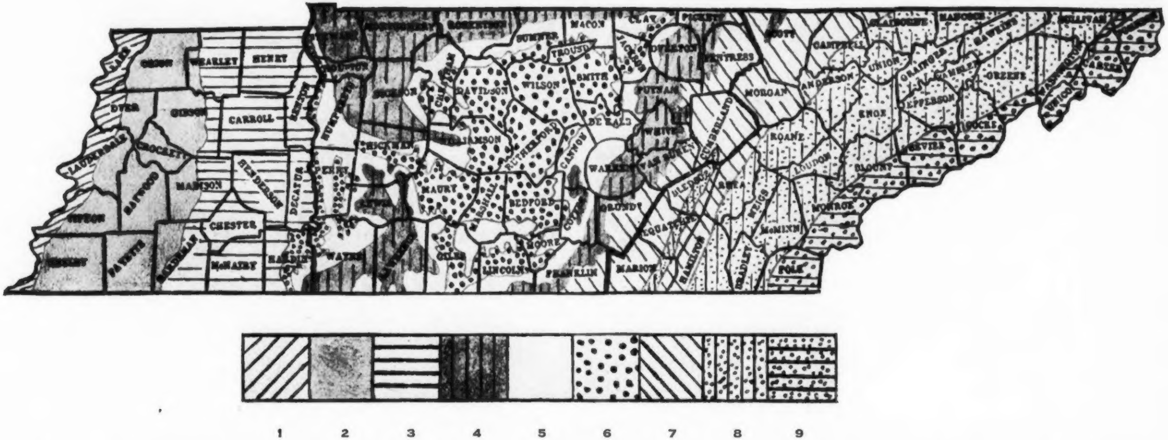
1 The author feels that this paper should have been written by Dr. H. K. Svenson, or at least he should have been a co-author, because of the great amount of time and work he spent in compiling the great bulk of the critical material.



Map 1.—1, Mississippi alluvium.* 2, Loess.* 3, Sandy loams, "Orange sands." Shallow loess over coastal plain sediments. Washes ruinously when neglected.* 4, Red and yellow clay loams derived from mountain limestone. 5, Interior Low Plateau Province, "Highland Rim." Sandy and sandy loam soils overlying clayey silt subsoils; barrens and like areas. 6, Nashville Basin. Heavy clay loams derived from calcareous and clay formations. 7, Appalachian Plateau Province, "Cumberland Plateau." Light sandy loams overlying fine yellow or red clay silt subsoil derived from shales and sandstones. 8, Tennessee Ridge and Valley Province, the "Great Valley" made up of parallel ridges and valleys, of most complex geology. Valleys mostly of heavy clay loams of calcareous and clay derivation as found in the Nashville Basin and Knox dolomite which also gives rise to heavy clay soils. Some of the higher ridges of the north end of the valley are capped with sandy loams derived from sandstones. Many ridges are cherty and in Jefferson, Greene, and Hawkins counties there are also tilted calcareous shaley ridges. 9, The Blue Ridge Province. A complex of slaty conglomerates, sandstones, shales, granites and gneisses giving rise to sandy to gravelly loams and coarse gravelly soils.

* 1, 2, 3 constitute the Coastal Plain Province.

The Highland Rim is a large area surrounding the Central Basin. It has an elevation of 800-1000 feet, and varies from gently undulating to hilly. The outer portion of the Rim is of limestone origin while the inner portion is siliceous.

West Tennessee slopes gradually from the Highland Rim to the Mississippi River. The elevation varies from 400 to 600 feet. The surface for the most part is gently undulating. The hilly portions are characterized by lower and more rounded hills than those found in other portions of the State. Loess deposits extend in a belt of 20 to 25 miles in width paralleling the Mississippi River. The soils of this region are primarily of sandstone origin, mostly of the Ruston series, which is very deficient in the essential plant nutrients.

Taken as a whole, this description of the State throws light on the unique place that Tennessee holds in the variability of its flora, which is due largely to the great variety of soils, and of habitats which range from prairie, swamplands, and alluvial woods of the west to the high mountain summits of the eastern portion.

This range of altitude from 400 feet to 6,600 feet affects the distribution of all species, especially the "southern" and "northern." The great majority of species represented are common in the eastern half of the United States. Most of the northern species found in the State are in the mountain areas of East Tennessee. These include—

C. diandra	*C. lucorum*	*C. strictior*
C. trisperma	*C. plantaginea*	*C. torta*
C. brunnescens	*C. leptonervia*	*C. folliculata*
C. angustior	*C. gracillima*	*C. rostrata*
C. Crawfordii	*C. flexuosa*	*C. Baileyi*
C. normalis	*C. scabrata*	

Northern species of general or local distribution in other parts of the State are—

C. eburnea	*C. albursina*	*C. glaucodea*
C. platyphylla	*C. Haleana*	*C. Swanii*

Southern species, in all probability, are best developed in the Coastal Plain areas, though they probably had their origin in the early Cretaceous times, when the present mountain area was a base-level land. During Cenozoic times and since then, this base-level land was uplifted. Our conception of a Coastal Plain species, therefore, requires some alteration—and we need to be reminded that these species probably had their origin in the interior millions of years ago. Perhaps we should then include all southern species extending northward into Tennessee with the "typically" Coastal Plain species, though the writer prefers to separate them on the basis of best development, in which case the southern species could be divided into the following two groups:

Best-developed on Coastal Plain:

C. Longii	*C. crebriflora*	*C. hyalinolepis*
C. albolutescens	*C. Joorii*	*C. louisianica*
C. Emmonsii	*C. glaucescens*	*C. gigantea*
C. styloflexa	*C. Barrattii*	
C. striatula	*C. Mitchelliana*	

Not best developed in Coastal Plain:

C. texensis	*C. abscondita*	*C. oxylepis*
C. Crus-corvi	*C. amphibola*	*C. cherokeensis*
C. nigro-marginata	*C. flaccosperma*	*C. complanata*

Another group, the Appalachian species, is represented by only a few, which range practically the whole length of the system, or are restricted to lesser areas in it.

C. radiata	*C. prasina*	*C. virescens*
C. aestivalis	*C. allegheniensis*	

The last is a small and interesting group of endemics. These are restricted to the southern part of the Appalachian system and include:

C. Ruthii	*C. purpurifera*
C. austro-caroliniana	*C. misera*

The range of elevations at which any species is found naturally varies. The author has found it more convenient to divide this range arbitrarily into three parts—low, medium, and high. The lower elevations are from 400 to 800 feet, the medium from 800 to 2,200 feet, and the higher from 2,200 to 6,600 feet. These ranges of elevation are not strictly adhered to by most species.

Some specimens numbered prior to the Morrill Hall fire at the University of Tennessee, January 18, 1934, were saved, as well as a record of collections. Most of the reports and collections by A. Gattinger, F. Lamson-Scribner, A. Ruth, T. H. Kearney, and S. M. Bain are incorporated in this paper.

The following abbreviations indicate the place of deposit of each specimen cited:

B.—Herbarium of the Brooklyn Botanic Garden.
N.Y.—Herbarium of the New York Botanical Garden.
U.—Herbarium of J. K. Underwood, Knoxville, Tennessee.
T.—Herbarium of the University of Tennessee at Knoxville.

An asterisk indicates no specimen now available, though there are records of specimens having been collected of many so indicated. It is desired that these records be preserved in this paper.

Only those species known to occur in the State, as represented by specimens or authentic collections, or those which are not known by the writer to have been collected but which probably occur in Tennessee, are included in the notes and keys.

The writer is greatly indebted to Dr. H. K. Svenson, Brooklyn Botanic Garden, for the loan of material and for other aid in compiling this paper. Thanks are due to Maud H. Purdy for the drawings; also to Dr. A. J. Sharp and Dr. Stanley A. Cain for their valuable suggestions and editing.

Many specimens of the Brooklyn Botanic Garden, collected by H. K. Svenson and seen by the author, were previously determined by F. J. Hermann of the U.S.D.A., as was some critical material from the University of Tennessee Herbarium.

ARTIFICIAL KEY TO SECTIONS OF TENNESSEE CARICES

1. Spike one.
  2. Perigynia strongly inflated; pistillate scales persistent..*C. squarrosa* in 34. SQUARROSAE, 641
  2. Perigynia not inflated.
    3. Perigynia rounded and beakless at apex, many-nerved..9. POLYTRICHOIDEAE, p. 626
    3. Perigynia not rounded at apex, beakless or beaked....................13. PICTAE, p. 628
1. Spike more than one.
  4. Stigmas two; achenes lenticular.
    5. Lateral spikes sessile, short (rarely elongate).
      6. Perigynia not whitish-puncticulate.
        7. Spikes androgynous.
          8. Perigynia with body abruptly contracted into the beak; culms not flattening in drying.
            9. Spikes few, or if more than 10, the spikes appearing greenish; sheaths not red-dotted ventrally............................1. BRACTEOSAE, p. 619
            9. Spikes numerous, the spikes appearing yellowish or brownish; sheaths often red-dotted ventrally, at least at the mouth.
              10. Perigynia yellowish or straw-colored, or in age black, plano-convex; sheaths usually transversely rugulose ventrally...2. MULTIFLORAE, p. 622
              10. Perigynia brownish, thick-plano-convex or unequally biconvex; leaf-sheaths not transversely rugulose ventrally..3. PANICULATAE, p. 622
          8. Perigynia with body tapering into the beak, or, if abruptly contracted, culms flattened in drying; perigynia yellowish, or, in one species, greenish..4. VULPINAE, p. 623
        7. Spikes not androgynous, the upper gynaecandrous, rarely staminate, the lateral gynaecandrous or pistillate, or very rarely with some staminate or androgynous spikes mixed in a head with gynaecandrous or pistillate spikes.
          11. Perigynia at most thin-edged, the lower part of body spongy-thickened.
            12. Perigynia spreading or ascending at maturity....6. STELLULATAE, p. 624
            12. Perigynia appressed...7. DEWEYANAE, p. 624
          11. Perigynia narrowly to broadly wing-margined, the lower part of body not spongy-thickened...8. OVALES, p. 625
      6. Perigynia whitish-puncticulate, not wing-margined, spongy-thickened at base; upper spikes gynaecandrous; culms in stools, but rootstocks often slender and prolonged...5. HELEONASTES, p. 623
    5. Lateral spikes peduncled, or if sessile elongate; terminal spike staminate or if rarely gynaecandrous or androgynous the lateral spikes peduncled.
      13. Achenes jointed with style; perigynia not lustrous.
        14. Achenes not constricted in the middle............................29. ACUTAE, p. 639
        14. Achenes constricted in the middle......................30. CRYPTOCARPAE, p. 639
      13. Achenes continuous with style; perigynia lustrous..........35. VESICARIAE, p. 641
  4. Stigmas three, achenes triangular.
    15. Perigynia pubescent, puberulent, hispid, granular roughened, or scabrous.
      16. Style jointed with achene, at length withering and deciduous.
        17. Achenes with sides convex above, closely enveloped in upper part of perigynium-body; bracts of non-basal pistillate spikes sheathless or very nearly so; pistillate spikes 3-25-flowered; lowest scale usually not rough awned; perigynia with short to long slender beaks..11. MONTANAE, p. 627
        17. Achenes with flat or concave sides.
          18. Bracts of non-basal pistillate spikes sheathing, the blades absent or rudimentary, the sheaths more or less purplish-tinged; achenes closely enveloped, filling perigynium body.

19. Perigynia prominently two-keeled, otherwise nerveless............ ....12. DIGITATAE, p. 628
19. Perigynia many-nerved or many-ribbed..............13. PICTAE, p. 628
18. Bracts sheathing or sheathless, the blades well developed.
20. Bracts sheathless or the lower short-sheathing.
21. Perigynia pubescent.
22. Leaves not septate-nodulose; perigynia at most shallowly bidentate, style very short, thickish.................. ....23. VIRESCENTES, p. 636
22. Leaves septate-nodulose; perigynia strongly bidentate or sometimes only obliquely cut; achene loosely enveloped; style slender......................24. HIRTAE, p. 638
21. Perigynia granular-roughened or scabrous; style slender; achene not closely enveloped, the upper part of perigynium body empty.
23. Perigynia nearly beakless................27. PENDULINAE, p. 638
23. Perigynia strongly beaked..................25. ANOMALAE, p. 638
20. Bracts, at least the lower ones, long sheathing.
24. Perigynia with beak not strongly bidentate.
25. Pistillate spikes short, oblong to linear, erect, or, if drooping, the spikes short and the perigynia acutely triangular......................................16. LAXIFLORAE, p. 629
25. Pistillate spikes elongate, linear to cylindric, slender-peduncled, the lower widely spreading or drooping ....21. SYLVATICAE, p. 635
24. Perigynia with beak strongly bidentate; culms never lateral; scales not strongly dark-tinged....24. HIRTAE, p. 638
16. Style continuous with the achene, indurated and persistent.
26. Perigynia less than 1 cm. long, subcoriaceous........33. PALUDOSAE, p. 640
26. Perigynia 1 cm. long or more, membranaceous ....*C. Grayi* in 36. LUPULINAE, p. 642
15. Perigynia glabrous.
27. Style jointed to the achene, not indurated, at length withering.
28. Achenes slightly depressed at summit, constricted at base, the sides convex above; staminate scales with margins united at base............ ....10. PHYLLOSTACHYAE, p. 626
28. Achenes more or less strongly apiculate-tipped, not constricted at base; staminate scales with margins separate to base.
29. Lower bracts (at least) long-sheathing.
30. Bracts bladeless or with rudimentary blades.
31. Leaf-blades filiform.......................................14. ALBAE, p. 628
31. Leaf-blades not filiform.........................16. LAXIFLORAE, p. 629
30. Bracts with well-developed blades.
32. Foliage, especially sheaths, pubescent.
33. Perigynia beakless or short-beaked; terminal spike gynaecandrous..............................20. GRACILLIMAE, p. 633
33. Perigynia conspicuously or strongly beaked.................... ....21. SYLVATICAE, p. 635
32. Foliage not pubescent.
34. Perigynia with beak not bidentate, at most emarginate.
35. Pistillate spikes short, oblong to linear, erect, or if drooping the spikes short and the perigynia acutely triangular.
36. Perigynia with few to many strong raised nerves or nerveless.
37. Perigynia tapering at base, triangular; achenes closely enveloped.
38. Rootstock elongate, often sending out

long horizontal stolons..15. PANICEAE, p. 628
38. Rootstock not elongate, not sending out long horizontal stolons..16. LAXIFLORAE, p. 629
37. Perigynia rounded at base, suborbicular in cross-section; achenes loosely enveloped ....17. GRANULARES, p. 632
36. Perigynia with numerous fine impressed nerves.
39. Perigynia tapering at base, constricted at apex, obtusely triangular; achenes closely enveloped..................18. OLIGOCARPAE, p. 632
39. Perigynia rounded at both ends, in cross-section orbicular................19. GRISEAE, p. 632
35. Pistillate spikes elongate, linear to cylindric, slender-peduncled, the lower drooping.
40. Perigynia beakless or short-beaked; terminal spike often gynaecandrous..20. GRACILLIMAE, p. 633
40. Perigynia conspicuously or strongly beaked.
41. Culms strongly reddish-tinged at base, aphyllopodic................21. SYLVATICAE, p. 635
41. Culms not strongly reddish-tinged at base, phyllopodic; pistillate spikes dense, many-flowered; perigynia 5-6 mm. long, more or less inflated, the beak becoming bidentate..........................22. LONGIROSTRES, p. 636
34. Perigynia with beak bidentate, obliquely cut, at length bidentate....................................22. LONGIROSTRES, p. 636
29. Lower bracts sheathless or very short-sheathing.
42. Leaves not septate-nodulose.
43. Perigynia beakless or very short-beaked; pistillate spikes 1-2.5 cm. long..28. LIMOSAE, p. 639
43. Perigynia prominently beaked; pistillate spikes large, many-flowered......................................25. ANOMALAE, p. 638
42. Leaves septate-nodulose...............................26. SHORTIANAE, p. 638
27. Style continuous with the achene and of the same bony texture, not withering.
44. Perigynia lanceolate or subulate-lanceolate, tapering into the beak, many nerved...31. FOLLICULATAE, p. 640
44. Perigynia broader, abruptly contracted into the beak, usually strongly ribbed.
45. Perigynia finely and closely ribbed........32. PSEUDO-CYPEREAE, p. 640
45. Perigynia coarsely ribbed.
46. Perigynia subcoriaceous and firm................33. PALUDOSAE, p. 640
46. Perigynia membranaceous.
47. Perigynium-body obovoid or obconic, truncately contracted into the prominent beak........34. SQUARROSAE, p. 641
47. Perigynium-body obovoid or globose-ovoid, not truncately contracted.
48. Perigynia less than 1 cm. long..........35. VESICARIAE, p. 641
48. Perigynia 1 cm. long or longer........36. LUPULINAE, p. 642

Section 1. Bracteosae

1. Sheaths tight, inconspicuously if at all green-and-white-mottled or septate-nodulose dorsally.
2. Perigynium-body with lower third to half corky-thickened; perigynia usually widely radiating or reflexed at maturity.

3. Beak of perigynium smooth; scales acuminate, deciduous; spikes except lower 1-3 aggregated.
   4. Body of perigynium broadly ovate, unequally biconvex, deep-green, many-striate at base ventrally, abruptly short-beaked; leaf-blades 1-3 mm. wide .... 1. *C. retroflexa*
   4. Body of perigynium lanceolate or ovate-lanceolate, plano-convex, light-green, nerveless, tapering to a conspicuous beak; leaf-blades 0.75-1.5 mm. wide .... 2. *C. texensis*
3. Beak of perigynium serrulate; scales obtuse or acutish, persistent; spikes except the upper one separate.
   5. Stigmas slender, usually not twisted, elongate, light-brownish-red; perigynia light-green, tapering or but little contracted into the beak, inconspicuously white-hyaline at the orifice .... 3. *C. rosea*
   5. Stigmas stouter, twisted, short, deep-brownish-red; perigynia deep-green, abruptly contracted into the beak, conspicuously white-hyaline at the orifice.
      6. Leaf-blades 1.5-3 mm. averaging 2.5 mm. wide; spikes with 6-20, usually 9-12, perigynia; perigynia 3.25-4.5 mm. long, widely spreading .... 4. *C. convoluta*
      6. Leaf-blades 1-1.75 mm. averaging about 1 mm. wide; spikes with 2-6 perigynia; perigynia 2.25-3 mm. long, more ascending; lowest bract strongly developed .... 5. *C. radiata*

2. Perigynium-body inconspicuously corky-thickened at base.
   7. Inflorescence ovoid, oblong-ovoid, or suborbicular, the spikes densely capitate.
      8. Scale (excluding awn) much exceeded by perigynium-body.
         9. Perigynia with raised margins ventrally, narrowly to broadly ovate, round-tapering at base, broadest below middle; scales acuminate to aristate; sheaths slightly thickened at mouth; culms densely cespitose .... 6. *C. cephalophora*
         9. Perigynia flat ventrally, broadly ovate, broadest at the truncate-cordate base; scales acute to cuspidate; head 8-20 mm. long; scales greenish-hyaline with green midvein; culms densely cespitose, frequently procumbent; sheaths not thickened at mouth, not cross-rugulose ventrally .... 7. *C. Leavenworthii*
      8. Scale (excluding awn) from little shorter to exceeding perigynium-body; sheaths thickened at mouth, root-stocks short-creeping.
         10. Culms normally spreading; perigynia lightly nerved dorsally; stigmas short .... 8. *C. mesochorea*
         10. Culms stiff, erect; perigynia ribbed dorsally; stigmas long. Depauperate forms of .... 10. *C. plana*
   7. Inflorescence oblong or linear-oblong to elongate and interrupted, not capitate.
      11. Perigynia strongly ribbed and very low-convex ventrally, the margins slightly raised; achenes suborbicular .... 9. *C. Muhlenbergii*
      11. Perigynia nerveless or short-nerved at base and flat ventrally, the margins not raised .... 10. *C. plana*

1. Sheaths conspicuously green-and-white-mottled and septate-nodulose dorsally, loose, membranaceous and usually easily breaking ventrally; perigynia deep green, with raised margin ventrally; leaf-blades 5-10 mm. wide; lower spikes usually separate; ligule wider than long; stigmas short .... 11. *C. sparganioides*

1. CAREX RETROFLEXA Muhl.

Woods and cedar glades overlying limestone at lower through medium elevations; common.

Davidson Co.—*Gattinger**; *Svenson*, B. 9065; Franklin Co.—*Svenson*, B. 7558, 10035; Knox Co.—*Underwood*, U. 4487.

2. CAREX TEXENSIS (Torr.) L. H. Bailey

Dry open woodlands, cedar glades, shaded lawns and pastures at lower through medium elevations; common.

Davidson Co.—*Svenson*, B. 9068; Franklin Co.—*Svenson*, B. 10012; Grainger Co. —*Underwood*, U. 4200; Hamilton Co.—*Jennison**; Knox Co.—*Anderson*,* and *Underwood*, U. 4449; Lincoln Co.—*Svenson*, B. 9962; Sevier Co.—*Cain*, T. This species and *C. retroflexa* intergrade.

3. CAREX ROSEA Schk.

Woodlands, and shaded stream banks from lower through higher elevations; frequent.

Blount Co.—*Underwood*, U.; Cumberland Co.—*Underwood*, U. 2845; Franklin Co.—*Svenson*, B. 9997; Knox Co.—*Underwood*, U.; Morgan Co.—*Svenson*, B. 9320; Sevier Co.—*Underwood*, U.; Sumner Co.—*Gattinger**; Wilson Co.—*Gattinger*.*

4. CAREX CONVOLUTA Mackenzie

Dry woods at lower and medium elevations; infrequent.

Cannon Co.—*Svenson*, B. 9273; Franklin Co.—*Svenson*, B. 7573. Grainger Co.—*Sharp*, T. 1620; Johnson Co.—*Underwood*, U. 49(a); Morgan Co.—*Underwood*, U. 7; Rhea Co.—*Sharp*, T. 3416; Sevier Co.—*Jennison*, T.

5. CAREX RADIATA (Wahl.) Dewey

Woods, from lower to highest elevations; frequent, especially in the mountains.

Blount Co.—*Jennison*, T.; Johnson Co.—*Underwood* and *Sharp*, U. 86; Sevier Co. —Cain, T.; *Underwood*, T. 1976.

6. CAREX CEPHALOPHORA Muhl.

Dry woods, lower to medium elevations; common.

Blount Co.—*Kinsey*, T.; Cheatham Co.—*Svenson*, B. 10203; Cumberland Co.—*Underwood*, U. 2848; Davidson Co.—*Gattinger**; *Svenson*, B. 9715; Fentress Co.—*Underwood* and *Sharp*, T.; Franklin Co.—*Svenson*, B. 8721; Grainger Co.—*Underwood*, U.; Hamilton Co.—*Sharp*, T. 1059; Johnson Co.—*Underwood* and *Sharp*, T.; Knox Co.—*Ruth*, T.; *Underwood*, U. 4486; *Morrison*, T.; *Sharp*, T.; Maury Co.—*Svenson*, B. 9053; Morgan Co.—*Underwood*, T.; *Jennison*, T. 1171; Rhea Co.—*Sharp*, T. 1053; Roane Co.—*Underwood*, U. 2770; Sumner Co.—*Weatherby*, T.

7. CAREX LEAVENWORTHII Dewey

Dry open woodlands, low moist places and banks at lower elevations; abundant in limestone area of Middle Tennessee. Weed in lawns.

Davidson Co.—*Svenson*, B. 9069; Franklin Co.—*Svenson*, B. 7634, 10013; Giles Co.—*Svenson*, B. 8813; Grundy Co.—*Svenson*, B. 9123; Hamilton Co.—*Churchill*, T.; Knox Co.—*Ruth*, T.; Lewis Co.—*Svenson*, B. 8795; Lincoln Co.—*Svenson*, B. 9965.

8. CAREX MESOCHOREA Mackenzie

Fields and dry wooded knolls at lower elevations; rare.

Knox Co.—*Ruth*, N. Y. 107 and 10925.

9. CAREX MUHLENBERGII Schk.

Dry hillsides and open wooded slopes at medium to higher elevations; infrequent.

Davidson Co.—*Gattinger**; Johnson Co.—*Sharp*, T.

10. CAREX PLANA Mackenzie

Dry open or wooded hillsides and cedar glades, especially frequent in siliceous regions of Highland Rim at medium elevations; infrequent elsewhere.

Cheatham Co.—*Svenson*, B. 9033; Coffee Co.—*Svenson*, B. 9153; Davidson Co.—*Svenson*, B. 7316 and 9064; Franklin Co.—*Svenson*, B. 9990; Hamilton Co.—*Churchill*, T.; Marion Co.—*Underwood*, T. 2515; Sevier Co.—*Underwood*, T.*

11. CAREX SPARGANIOIDES Muhl.

Dry woods and thickets especially in calcareous regions at lower elevations; infrequent.

Cumberland Co.—*Underwood*, U.; Knox Co.—*Underwood*, U.; Loudon Co.—*Sharp*, U. 4498.

Section 2. Multiflorae

Beak of perigynium much shorter than body; leaves normally shorter than the culm .... 12. *C. annectens*

Beak of perigynium about equalling the body, teeth of perigynia subulate-triangular, sharp; leaf-blades normally exceeding culms, very rough, long-tapering........ 13. *C. vulpinoidea*

12. CAREX ANNECTENS Bickn.

Dry fields, and pastures at lower elevations; infrequent.

Anderson Co.—*Underwood*, U. 88; Coffee Co.—*Svenson*, B. 10122; Davidson Co. *Svenson*, B. 9447; Franklin Co.—*Svenson*, B. 10230; Shelby Co.—*Moore*, T. Intergrades with *C. brachyglossa*.

13. CAREX VULPINOIDEA Michx.

Swamps and banks of streams at lower and medium elevations; common.

Blount Co.—*Greene*, T.; *Cain*, T. 1669; *Sharp*, T.; Carter Co.—*Gayle*, T.; Cheatham Co.—*Svenson*, B. 7161; Coffee Co.—*Svenson*, B. 7104; Davidson Co.—Gattinger*; *Svenson* and *Shaver*, B. 7436; Dickson Co.—*Svenson*, B. 10307; Giles Co.—*Svenson*, B. 8815a; Grainger Co.—*Sharp*, T. 1638; Haywood Co.—*Bain**; Johnson Co.—*Underwood*, U. 3349; Knox Co.—*Lamson-Scribner**; *Underwood*, T.; *Sharp*, T. 1777; Ludon Co.—*Sharp*, T.; Meigs Co.—*Underwood*, T. 2327; Morgan Co.—*Underwood*, T. 1364; Sevier Co.—*Jennison*, T.; *Underwood*, U. 1988; *Cain*, T.; Union Co.—*Morrison*, T.; Washington Co.—*Sharp*, T. 3805.

Section 3. Paniculatae

Perigynia very abruptly short-beaked, tapering at base; leaf-blades 2.5-8 mm. wide .... 14. *C. decomposita*

Perigynia tapering or contracted into the beak, rounded or truncate at base; leaf-blades 1-6 mm. wide .... 15. *C. diandra*

14. CAREX DECOMPOSITA Muhl.

Wet meadows and swamps, at lower elevations; rare.

Kearney, Wolf Creek, Cocke Co., May 14, 1893.*

15. CAREX DIANDRA Schrank

Wet meadows usually in calcareous regions; rare.

A. Gattinger's specimen was seen by the writer before the fire destroyed it. The label stated "In the mountains about Ducktown, Polk Co., 1878." The

species is so distinct that there could be little doubt of its having been recognized. It has a wide distribution, not only in Eurasia, but it has been recorded from New Zealand. Though there are no existing collections in any herbaria from Tennessee as far as the author knows, under these circumstances we feel it should be included in this publication.

Section 4. Vulpinae

Perigynia tapering into the beak, about the length of body or longer, the body obscurely to strongly nerved ventrally.
 Perigynium 4-6 mm. long, strongly nerved ventrally, rounded at base, membranaceous, the beak 1-2 times length of the body; sheaths not purplish-dotted ventrally; achenes ovate-orbicular.
  Sheaths cross-rugulose ventrally, easily broken, prolonged upward at mouth beyond base of blade, not thickened at the mouth........................16. *C. stipata*
  Sheaths not cross-rugulose ventrally or only obscurely so, not easily broken, not prolonged upward at mouth beyond base of blade, thickened at mouth ....17. *C. laevivaginata*
 Perigynium 6-7 mm. long, obscurely nerved ventrally, with a disk-like subcoriaceous base, the beak 2-3 times the length of the body; sheaths conspicuously purplish-dotted ventrally; achenes strongly ovate, tapering above ....18. *C. Crus-corvi*
Perigynium contracted into a beak not longer than the body, the body nerveless ventrally except at base ....19. *C. conjuncta*

16. CAREX STIPATA Muhl.

Swamps and wet meadows, from medium to high elevations; infrequent.

Carter Co.—*Cain*, T. 538; Johnson Co.—*Underwood* and *Sharp*, T; Lewis Co.—*Svenson*, B. 8798; Sevier Co.—*Cain*, T.; Underwood, U.

17. CAREX LAEVIVAGINATA (Kukenth.) Mackenzie

Swamps and wet woods at medium to higher elevations; rare.

Johnson Co.—*Underwood* and *Sharp*, U. 85, and T.; Knox Co.—*Underwood*, U.; Sevier Co.—*Sharp*, T.; *Underwood*, U.

18. CAREX CRUS-CORVI Shuttw.

Swamps at lower elevations, West Tennessee; infrequent.

Haywood Co.—*Bain*, N. Y. 497 and 783; Obion Co.—*Bain*.*

19. CAREX CONJUNCTA Boott.

Moist alluvial thickets mostly in calcareous districts at medium to high elevations; rare.

A collection made by the author at Henderson Springs, Sevier Co., May 2, 1930, was checked by K. K. Mackenzie. The specimen was later lost in the Morrill Hall fire.

Section 5. Heleonastes

Perigynia strongly many-nerved ventrally, 2.5-3.75 mm. long; beak obliquely cut, smooth or nearly so; achene oval-oblong........................20. *C. trisperma*
Perigynia nearly nerveless ventrally, 2-2.5 mm. long; beak minutely bidentate, serrate; achene ovate-orbicular ....21. *C. brunnescens*

20. CAREX TRISPERMA Dewey

Sphagnum bogs and wet acid woods, at higher elevations in mountains of

North Carolina where the first specimens of this species seen by the writer were collected by A. J. Sharp at Pineola, Avery Co., N. C. Records show that *H. M. Jennison* collected this species on the Bote Mt. road, Blount Co., at 4700 ft. elevation, T. 2568, July 2, 1936, but no such specimen could be found in the filled material of the herbarium. The specimen was identified by the author.

21. CAREX BRUNNESCENS (Pers.) Poir.

Boggy thickets, exposed ledges and woods in acid soils at medium to highest elevations in East Tennessee; common.

Blount Co.—*Jennison*, T.; Hamilton Co.—*Churchill*, T.; Sevier Co.—*Cain*, *Sharp*, *Underwood*, T.

Section 6. Stellulatae

Body of perigynium suborbicular or very broadly ovate, deep green at maturity, strongly nerved ventrally, the beak less than half the length of the body........................22. *C. incomperta*

Body of perigynium ovate to lanceolate, straw-colored at maturity or often darker-tinged, the beak half the length of body or more.

Perigynium with body noticeably exceeding the obtuse to acutish scale; leaf-blades averaging 3-3.5 mm. wide; sheaths strongly thickened at the mouth........................23. *C. Ruthii*

Perigynium with body equalled or exceeded by the scale; leaf-blades 0.75-2 mm. wide; sheaths scarcely thickened at mouth........................24. *C. angustior*

22. CAREX INCOMPERTA Bicknell

Acid soils and swampy woods at medium to higher elevations in East and Middle Tennessee; rare. See fig. 2 of plate.

Fentress Co.—*Underwood*, U. 2868; Franklin Co.—*Svenson*, B. 10128; Grundy Co.—*Svenson*, B. 7134; *Sharp* and *Underwood*, U. 49; Lewis Co.—*Svenson*, B. 8801; Marion Co.—*Svenson*, B. 8890; Putnam Co.—*Svenson*, B. 6865, 10452.

23. CAREX RUTHII Mackenzie

Swales and wet thickets at higher elevations of East Tennessee; rare.

Blount Co.—*Sharp* and *Jennison*, T.; Sevier Co.—Jennison, *Underwood*, *Sharp*, and *Cain*, T.

24. CAREX ANGUSTIOR Mackenzie

Johnson Co.—*Underwood*, *Sharp*, swampy meadows at 2800 ft. elevation, Shady Valley, U. 48, T. 846, 1573.

Section 7. Deweyanae

25. CAREX BROMOIDES Schk.

Swampy woods, medium to higher elevations in East Tennessee; rare.

Jennison, near Deal's Gap, Blount Co., 1800 ft. elevation, May 1, 1936, T.; *Sharp*, near Gatlinburg, Sevier Co., June 14, 1930, U.; *Underwood*, Mt. LeConte, Sevier Co., 3500 ft. elevation, June 1930, U.; *Cain*, "Sinks" of Little River, Sevier Co., April 25, 1934, T.; Pinnacle Mt., Sevier Co., 3000 ft. elevation, May 23, 1934, T.

Section 8. Ovales

1. Wing of perigynium not narrowed near middle of body; leaf-blades of sterile culms erect or ascending, usually clustered toward the top; sterile culms often poorly developed.
  2. Perigynia widest near middle or base, not obovate.
    3. Perigynia lanceolate-subulate to narrowly ovate-lanceolate, 3-4 times as long as wide.
      4. Perigynia lanceolate-subulate, 0.5-1.2 mm. wide, 4 mm. long, the margin nearly obsolete at base........26. *C. Crawfordii*
      4. Perigynia lanceolate to narrowly ovate-lanceolate, 1.2-2 mm. wide, 4-6.5 mm. long, noticeably wing-margined at base........27. *C. scoparia*
    3. Perigynia ovate-lanceolate or broader, at most twice as long as wide.
      5. Perigynia ovate, twice as long as wide, (3-4 mm. long, 1.5-2 mm. wide); perigynia and scales green or the scales light-yellowish-brown-tinged; achenes 1 mm. wide; sheaths conspicuously prolonged beyond base of blade at the mouth, green-and-white-mottled dorsally, the blades 2.5-6 mm. (usually 3.5-4.5 mm.) wide........28. *C. normalis*
      5. Perigynia 4-5.5 mm. long, 2.25-3.5 mm. wide, the body suborbicular.
        6. Achenes suborbicular, 1.25 mm. wide; perigynia ovate, submembranaceous, few-nerved ventrally, broadest near base, the beak broader than in *C. brevior*, especially toward the base........29. *C. molesta*
        6. Achenes orbicular at maturity, 1.5-1.75 mm. wide; perigynia broadly ovate to suborbicular, coriaceous, usually nerveless or nearly so ventrally, broadest near middle, abruptly contracted into a beak........30. *C. brevior*
  2. Perigynia obovate, the body widest near the top.
    7. Scales obtuse to short-acuminate; achenes substipitate; perigynia 1.5-2 mm. wide.
      8. Perigynia with body slightly rounded at the apex, not abruptly beaked; culms stiff........31. *C. Longii*
      8. Perigynia with body truncate-rounded at apex, abruptly beaked; culms slender to the base........32. *C. albolutescens*
    7. Scales long-acuminate or aristate; achenes slenderly stipitate; perigynia 2.5-4 mm. wide........33. *C. alata*
1. Wing of perigynium rather abruptly narrowed near middle of body; leaf-blades of sterile culms widely spreading, numerous, not clustered at the apex; sterile culms strongly developed........34. *C. tribuloides*

26. CAREX CRAWFORDII Fernald

Open grassy bank in moist or dry soil; rare.

Underwood, Roan Mt., Carter Co., 4600 ft. elevation, July 12, 1931, T.* A depauperate form, identified by K. K. Mackenzie.

27. CAREX SCOPARIA Schk.

Open swampy or moist places at medium to higher elevations; infrequent.

Underwood, Johnson Co. U. 36. *Sharp*, Clear Fork River near Rugby, Morgan Co., May 31, 1936. *Underwood*, Mt. LeConte, Sevier Co., June, 1930, U.

28. CAREX NORMALIS Mackenzie

Open, well-drained woodland in the higher mountains of East Tennessee; infrequent. Collections of this species in Tennessee cover a considerable range of variants.

Blount Co.—*Cain*, T.; Franklin Co.—*Svenson*, B. 9908—much slenderer than most material. Johnson Co.—Sharp, T. 3949; Sevier Co.—*Jennison*, T. 2655; Underwood, U. 235—so nearly like *C. projecta* Mackenzie that the specimen was identified as such by K. K. Mackenzie, 1930. It certainly is not typical *C. normalis* Mack. It appears this species has a southern complex which must not be taken too seriously from a purely taxonomic point of view.

29. CAREX MOLESTA Mackenzie

Dry open woodland or fields, calcareous or neutral soils at medium elevations; rare.

Davidson Co.—*Svenson*, open field on limestone near Nashville, May 7, 1939, B. 9988.

30. CAREX BREVIOR (Dewey) Mackenzie

Open woods and fields in dry, calcareous or neutral soils at medium elevations; rare. Mackenzie in North American Flora.

31. CAREX LONGII Mackenzie

Wet acid soils of medium elevations in East Tennessee; infrequent.

Cumberland Co.—*Underwood*, T. 3864; Fentress Co.—*Underwood*, U. 2870; Franklin Co.—*Svenson*, B. 10124; Grundy Co.—*Svenson*, B. 7135, 8734; Morgan Co.—*Sharp*, T. 1117. Putnam Co.—*Underwood*, U. 4070; Sequatchie Co.—*Svenson*, B. 8754.

32. CAREX ALBOLUTESCENS Schwein.

C. straminea of Mackenzie.

In acid soils in swampy woodlands at lower elevations; infrequent.

Coffee Co.—*Svenson*, B. 8720; Fentress Co.—*Svenson*, B. 9324; Franklin Co.—Svenson, B. 10219 (a narrow leaved form); Henderson Co.—*Bain*, N. Y. 10999; Morgan Co.—*Svenson*, B. 9008.

33. CAREX ALATA Torr.

Swampy meadows in non-acid or calcareous soils at medium elevations; rare.

Grundy Co.—*Svenson*, Goose Pond near Pelham, May 15, 1939, B. 10147.

34. CAREX TRIBULOIDES Wahl.

Wet meadows and banks of streams, well distributed over the state at most elevations; fairly common.

Anderson Co.—*Underwood*, U. 421; Blount Co.—*Jennison*, T. Chester Co.—*Bain**; Davidson Co.—*Svenson*, B. 7437; Giles Co.—*Svenson*, B. 8815; Grainger Co.—*Sharp*, T.; Grundy Co.—Svenson, B. 9115; Knox Co.—Underwood, U.; Loudon Co.—*Sharp*, T.; Morgan Co.—*Underwood*, U. 2783; Sevier Co.—*Underwood*, U. 1989; *Cain*, T.; *Jennison*, T.

Section 9. Polytrichoideae

35. CAREX LEPTALEA Wahl.

In bogs, wet meadows, and dolomitic slicks, lower to higher elevations; infrequent.

Blount Co.—*Jennison*, T.; Campbell Co.—*Underwood*, U. 167, 1451; Carter Co.—*Underwood*, U; Cheatham Co.—*Svenson*, B. 7165; Johnson Co.—*Underwood* and *Sharp*, U. 59; Knox Co.—*Underwood*, U.; Lawrence Co.—*Svenson*, B. 9548.

Section 10. Phyllostachyae

Body of perigynium oblong-oval; culm-angles minutely serrulate; pistillate flowers usually 3-10; staminate scales obtuse or acutish............................36. *C. Willdenovii*

Body of perigynium orbicular; culm-angles sharply serrulate; pistillate flowers usually 2 or 3; staminate scales truncate, erose ....37. *C. Jamesii*

36. CAREX WILLDENOVII Schk.

Dry woods, thickets, in siliceous soils, at lower to medium elevations; rare.

Cheatham Co.—*Svenson*, B. 10200; Franklin Co.—*Svenson*, B. 9986, 10036; Maury Co.—*Svenson*, B. 9052; Morgan Co.—*Underwood*, U. 1; *Svenson*, B. 9332.

37. CAREX JAMESII Schwein.

Dry woods in limestone districts at lower elevations; rare.

Davidson Co.—*Svenson*, B. 9072, cedar glades north of Mt. View, June 15, 1938. Gattinger reported it in the State.

Section 11. Montanae

1. Perigynium-body much longer than wide, very closely enveloping the achene.
  2. Perigynia 2.5-3.5 mm. long, conspicuous in the spikes, not nearly concealed by scales; sterile shoots mostly central; scales not strongly dark-margined.
    3. Culms erect usually more or less strongly exceeding leaves; staminate scales obtuse to short-acute, closely appressed, not cucullate at tip, the midvein usually not extending to tip; pistillate spikes more or less strongly separate .... 38. *C. artitecta*
    3. Culms weak, usually much shorter than, but at times somewhat exceeding leaves; staminate scales rather loose-tapering and cucullate at tip, the midvein extending to tip and there rough; pistillate spikes except lowermost closely contiguous........ 39. *C. Emmonsii*
  2. Perigynia 3-4 mm. long, inconspicuous in the spikes, nearly concealed by the scales; sterile shoots lateral; scales usually strongly dark-margined........ 40. *C. nigro-marginata*
1. Perigynium-body about as long as wide, less closely enveloping the achene.
  4. Plants loosely cespitose and without long horizontal stolons; ligule conspicuous, longer than wide; culms mostly aphyllopodic, not conspicuously fibrillose at base .... 41. *C. communis*
  4. Plants densely cespitose and with long horizontal stolons; ligule short, wider than long, or much wider; culms phyllopodic, conspicuously fibrillose at base.
    5. Perigynium-beak less than half the length of the body; achenes obovoid........ 42. *C. pennsylvanica*
    5. Perigynium-beak about as long as the body; achenes obovoid-orbicular........ 43. *C. lucorum*

38. CAREX ARTITECTA Mackenzie

C. varia Muhl.

Open woods and clearings in both siliceous and calcareous soils at low to higher elevations; frequent.

Blount Co.—*Underwood*, U.; Carter Co.—*Underwood*, U.; Cheatham Co.—*Svenson*, B. 10199; Franklin Co.—*Svenson*, B. 10040; Grainger Co.—*Sharp* and *Jennison*, T.; Hamilton Co.—*Sharp* and *Hesler*, T.; Knox Co.—*Underwood*, U.; *Wilson*, T. 124; Morgan Co.—*Svenson*, B. 4081; Putnam Co.—*Cain*, T.; Sevier Co.—*Underwood*, U. 671.

39. CAREX EMMONSII Dewey

C. albicans of some authors.

Open sandy woods and swamps at lower elevations; rare.

Franklin Co.—*Svenson*, swamp near Huntland, May 8, 1939, B. 10192; Coffee Co.—*Svenson*, confined to hummocks and stump bases in swamps, April 30, 1936, B. 7516.

40. CAREX NIGRO-MARGINATA Schw.

Dry woods both acid and alkaline soils at lower to medium elevations; infrequent.

Blount Co.—*Underwood*, U. 605; Cannon Co.—*Svenson*, B. 9289; Franklin Co.—*Svenson*, B. 7584, and 10027; Hamblen Co.—*Underwood*, U.; Hamilton Co.—*Churchill*, T.; Knox Co.—*Kearney**; Madison Co.—*Bain**; Union Co.—*Underwood*, U. 707.

41. CAREX COMMUNIS L. H. Bailey

Dry woodlands and bluffs, lower to higher elevations; infrequent.

Grainger Co.—*Drew*, T.; Grundy Co.—*Svenson*, B. 10155; Knox Co.—*Underwood*, U. 686; Marion Co.—*Svenson*, B. 10045; Morgan Co.—*Sharp*, T.; Sevier Co.—*Underwood*, U. 119; *Cain*, T.; Sullivan Co.—*Underwood*, U.; Union Co.—*Underwood*, U. 701.

42. CAREX PENNSYLVANICA Lam.

Open woodlands, and sunny banks in well-drained rocky soil from lower to high elevations; fairly common.

Blount Co.—*Jennison*, T.; *Cain*, T. 1449; Carter Co.—*Cain*, T.; Davidson Co.—*Gattinger**; Grainger Co.—*Sharp*, T. 142; Hamilton Co.—*Sharp*, T. 1003; Knox Co. —*Kearney**; Putnam Co.—*Cain*, T. 4384; Sevier Co.—*Jennison*, T.; *Underwood*, U.

43. CAREX LUCORUM Willd.

Well drained open woodland, at medium to higher elevations; infrequent.

Knox Co.—*Underwood*, U. 626; Marion Co.—Svenson, B. 10042; Sevier Co.—*Underwood*, U. 638; *Jennison*, T. 378; *Cain*, T.

Section 12. Digitatae

44. CAREX PEDUNCULATA Muhl.

According to Mackenzie its habitat is rich woods, usually in calcareous regions; rare.

Marion Co.—*Svenson*, B. 10048, wet sandstone bluffs with southern exposure, Big Fiery Gizzard Cove, east of Tracy City, May 13, 1939.

Section 13. Pictae

45. CAREX PICTA Steud.

Woods and ravines; localized but abundant in the ravines of the Highland Rim in Middle Tennessee.

Cheatham Co.—*Svenson*, B. 10475; Davison Co.—*Svenson*, and *Shaver*, B. 9611; Lawrence Co.—*Svenson*, B. 9550; Maury Co.—*Svenson*, B. 9051.

Section 14. Albae

46. CAREX EBURNEA Boott.

Soil habitat varied, open sunny banks to wooded siliceous or dolomitic bluffs at medium elevations; infrequent.

Anderson Co.—*Sharp*, T.; Cheatham Co.—*Svenson*, B. 4210 and 7194; Knox Co. —*Underwood*, U.; *Sharp*, T. 3315.

Section 15. Paniceae

47. CAREX MEADII (Dewey) Bailey

Moist open places in oak barrens at medium elevations; rare.

Coffee Co.—*Svenson*, B. 7515; Franklin Co.—*Svenson*, B. 9956.

Section 16. Laxiflorae

1. Bract-sheaths and base of culms and staminate scales strongly purple or red-tinged.

2. Pistillate spikes 2-6 flowered on long pendulous capillary peduncles; leaf-blades 3-12 mm. wide .... 48. *C. austro-caroliniana*

2. Pistillate spikes 3-12 flowered on erect peduncles; leaf-blades 7-25 mm. wide .... 49. *C. plantaginea*

1. Bract-sheaths not purple or red-tinged, base of culm rarely so; staminate scales greenish-white or reddish-brown tinged, or dull purplish-brown.

3. Perigynia sharply triangular, short-tapering at base, 35-50 nerved, hispidulous or minutely asperulous.

4. Pistillate spikes sessile or if peduncled the spikes not pendulous or drooping.

5. Leaf-blades up to 25 mm. wide; perigynia 1.75 mm. wide.... 50. *C. platyphylla*

5. Leaf-blades not over 9-10 mm. wide, perigynia 1.50 mm. wide .... 51. *C. abscondita*

4. Pistillate spikes drooping on long capillary peduncles.

6. Pistillate spikes without a staminate flower at the base; leaf-blades 2-5 mm. wide, erect, green .... 52. *C. digitalis*

6. Pistillate spikes with 1-2 staminate flowers at the base; leaf-blades 5-12 mm. wide, weak, glaucous-green .... 53. *C. laxiculmis*

3. Perigynia obtusely triangular (at least below), long-stipitate, glabrous.

7. Base of culm purplish or red-tinged.

8. Spikes not long-extended from sheaths; perigynia 3.75-4.25 mm. long .... 54. *C. purpurifera*

8. Spikes on filiform peduncles; perigynia 2.5-3.5 mm. long...... 55. *C. gracilescens*

7. Base of culm brownish-tinged or straw-colored.

9. Leaves of the fertile culms 2.5-3.5 mm. wide .... 56. *C. styloflexa*

9. Leaves of the fertile culms wider—up to 15 mm. or more wide.

10. Staminate spike strongly peduncled, exceeding the pistillate spike.

11. Perigynia 3-4.25 mm. long, 1.5 mm. wide, barely overlapping .... 57. *C. laxiflora*

11. Perigynia 4-5 mm. long, 2 mm. wide, more crowded in the spike. .... 58. *C. striatula*

10. Staminate spike sessile or nearly so, except sometimes more or less long-peduncled in *C. blanda* and sometimes short-peduncled in *C. crebriflora.*

12. Perigynium 2-ribbed, otherwise nerveless or faintly nerved, 1.5 mm. wide .... 59. *C. leptonervia*

12. Perigynium finely to strongly many-nerved, 1.75-2 mm. wide.

13. Leaf-blades of sterile shoots 3-8 mm. wide; beak of perigynium 1 mm. long, straight or slightly excurved .... 60. *C. crebriflora*

13. Leaf-blades of sterile shoots much wider; beak of perigynium 0.5 mm. long, abruptly bent or recurved.

14. Staminate spike linear, very slender, 1.25 mm. wide; sterile shoots reduced to tufts of leaves, not forming culms; pistillate scales obtuse or truncate, not awned or mucronate; all leaf-blades 7-30 mm. wide .... 61. *C. albursina*

14. Staminate spike linear-obclavate, sometime pistillate at the apex, 2-3 mm. wide; sterile shoots developing conspicuous culms; pistillate scales mucronate to long-awned; all leaf-blades 4-15 mm. wide .... 62. *C. blanda*

48. CAREX AUSTRO-CAROLINIANA L. H. Bailey

Mountain sides and gorges, siliceous soils in mountains of East Tennessee, and Cumberland Plateau, not rare in this region, but infrequent and localized. Our earliest species.

Blount Co.—*Morrison*, T. 109; Grundy Co.—*Svenson*, B. 10156; Marion Co.—

Svenson, B. 8896, 10046; Polk Co.—*Kearney**; Sevier Co.—*Underwood*, U. 422 and 2458; *Cain*, T.; *Jennison*, T. 533.

49. Carex plantaginea Lam.

Well drained, rich wooded slopes and rocky bluffs, usually in siliceous soil, but sometimes in limestone soils or bluffs at lower to medium elevations; infrequent and localized.

Blount Co.—*Jennison*, T.; DeKalb Co.—*Svenson*, B. 7238; Grundy Co.—*Svenson*, B. 10159; Polk Co.—*Small**; Putnam Co.—*Jennison*, T.; Sevier Co.—*Jennison*, T.; *Underwood*, U. 657, and 644; *Cain*, T.

50. Carex platyphylla Carey

Dry, open woods and slopes. All specimens listed collected on dry limestone or dolomitic bluffs at medium elevations; rare and localized.

Anderson Co.—*Sharp*, T. 3535; Knox Co.—*Underwood*, U. 696; Roane Co.—*Kearney**; Sullivan Co.—*Underwood* and *Sharp*, U. 329; Union Co.—*Underwood*, U. 705; *Sharp*, T. 3523.

51. Carex abscondita Mackenzie

Dry woodlands. This species has not been collected within the State to the writer's knowledge. Collected by *Svenson* over the Tennessee-Alabama state line in Jackson Co., Alebama, B. 10193.

52. Carex digitalis Willd.

Dry woods and thickets, from lower to higher elevations; fairly common.

Cannon Co.—*Svenson*, B. 9271; Cheatham Co.—*Svenson*, B. 10346; Franklin Co. —*Svenson*, B. 7578, 9689, 9985; Grundy Co.—*Svenson*, B. 7301; Johnson Co.—*Underwood* and *Sharp*, U. 58; Knox Co.—*Underwood*, U.; Lawrence Co.—*Svenson*, B. 9537; Marion Co.—*Svenson*, B. 10075; *Underwood* and *Sharp*, T.; Maury Co.—*Svenson*, B. 9047 (this specimen is *C. digitalis* var. *macropoda* Fernald); Montgomery Co.—*Svenson*, B. 9699; Morgan Co.—*Underwood*, U. 717; *Svenson*, B. 9331; Rhea Co.—*Sharp*, T.; Sevier Co.—*Underwood*, T. 666; *Sharp*, T.; *Cain*, T.; Union Co.—*Morrison*, T.

53. Carex laxiculmis Schw.

Dry woods, thickets, and alluvial deposits in woods, from lower to medium and lower reaches of higher elevations; rare.

Cannon Co.—*Svenson*, B. 9300; Grainger Co.—*Underwood*, U.; Johnson Co.—*Underwood*, *Sharp*, T. 3411; Morgan Co.—*Underwood*, U. 725; Sullivan Co.—*Underwood* and *Sharp*, T.

54. Carex purpurifera Mackenzie

Open wooded slopes not confined to calcareous soils, from lower to medium elevations of East Tennessee; rare. Type collected in Campbell Co.

Blount Co.—*Underwood*, U.; Campbell Co.—*John Bright*, Britton Herbarium; Cannon Co.—*Svenson*, B. 9301; Cocke Co.—*Sharp**; Franklin Co.—Svenson, B. 9691; Knox Co.—*Underwood*, U. 687.

55. Carex gracilescens Steud.

C. laxiflora var. *gracillima* Boott. of Gray's Man., ed. 7.

Dry or moist woods, cedar glades, calcareous regions and lower to medium

elevations; rare. A plant of the Ohio-Mississippi drainage. More abundant in the Nashville area than elsewhere.

All specimens of this species cited were collected by *Svenson*. Cheatham Co.—B. 10394; Grundy Co.—9916; Rutherford Co.—7704. Those specimens from Cheatham and Davidson Counties appear to be variants without purple tinge at base of culms and have a more slender habit.

56. CAREX STYLIFLEXA Buckl.

Woodlands at lower to medium elevations; infrequent.

Fentress Co.—*Underwood, Sharp*, T. 2204; Franklin Co.—*Svenson*, B. 10125; Knox Co.—*Underwood*, U.; Lawrence Co.—*Svenson*, B. 9546; Marion Co.—*Svenson*, B. 9514; Putnam Co.—*Svenson*, B. 10454; Sevier Co.—*Underwood*, U.

Old leaf margins have small retrorse spines; the staminate spike is slender.

57. CAREX LAXIFLORA Lam.

Dry rich woods, and thickets in siliceous soils, and lower to higher elevations; fairly common.

Bradley Co.—*Sharp*, T. 1099; Cannon Co.—*Svenson*, *C. laxiflora* var. *serrulata* Hermann, B. 9267; Coffee Co.—*Svenson*, B. 9949 (robust form, perhaps a polyploid); Franklin Co.—*Svenson*, B. 7733; Grainger Co.—*Jennison*, T. 359; Hamilton Co.—*Sharp*, T. 1002; Loudon Co.—*Sharp*, T. 4449; Marion Co.—*Svenson*, B. 8897, 10043, 10065 (robust form, *C. laxiflora* var. *serrulata* Hermann) 10081; Union Co.—*Morrison*, T.

58. CAREX STRIATULA Michx.

Well drained woodlands, lower to higher elevations; infrequent.

Blount Co.—*Jennison*, T. 2226; Cocke Co.—*Sharp*, T.; Grainger Co.—*Jennison*, T.; Knox Co.—*Underwood*, U.; Loudon Co.—*Sharp* and *Cain*, T.; Union Co.—*Underwood*, U. 706.

A species in the sterile soils of the coastal plain with rough, papillose leaves of preceding year and prominent staminate spikes.

59. CAREX LEPTONERVIA Fernald

Rich well drained woods, calcareous and siliceous soils, from lower to higher elevations; infrequent.

Blount Co.—*Jennison*, T.; Johnson Co.—*Underwood* and *Sharp*, U. 30; Sevier Co. —*Cain*, T.

60. CAREX CREBRIFLORA Wiegand

Moist woodlands. This species has not been collected within the State bounds to the writer's knowledge. Because of its being a south coastal plain and piedmont species with possible extensions northward as in other species, the author has included it.

61. CAREX ALBURSINA Sheldon

Wooded bluffs or slopes, mostly in calcareous soil at lower to medium elevations; infrequent.

Cannon Co.—*Svenson*, B. 9282, 9272; Cheatham Co.—*Svenson*, B. 7195 and 10431; Franklin Co.—*Svenson*, B. 7556; Knox Co.—*Underwood*, U.; Montgomery Co.—*Svenson*, B. 9707; Union Co.—*Morrison*, T.; Washington Co.—*Sharp*, T. 3835.

62. CAREX BLANDA Dewey

Moist and dry rich woodlands and thickets in both siliceous and calcareous soils; best developed on the latter type at lower to higher elevations; fairly common.

Cheatham Co.—*Svenson*, B. 10204 and 10205; Davidson Co.—*Svenson*, B. 9071 and 10007; Franklin Co.—*Svenson*, B. 10038 and 10031; Knox Co.—*Underwood*, U. 4508; Madison Co.—*Bain**; Marion Co.—*Jennison*, U.; Sevier Co.—*Jennison*, T.

Section 17. Granulares

Rootstocks not long-creeping; staminate spike short-peduncled or sessile; the two upper pistillate spikes usually contiguous.
  Perigynia elliptic-obovoid or elliptic-ovoid, 2-2.5 mm. long, 1.5 mm. wide, ascending, not ventricose-squarrose, membranaceous, nerved, sessile, rounded at apex, abrouptly very minutely beaked, light green, becoming yellowish-brown ....63. *C. Haleana*
  Perigynia broadly ovoid to broadly obovoid, 2.5-4 mm. long, 2-2.5 mm. wide, soon ventricose-squarrose, tapering at apex, minutely beaked, olive green or in age yellowish green ....64. *C. granularis*
Rootstocks long-creeping; staminate spike long-peduncled; spikes all widely separate ....65. *C. Crawei*

63. CAREX HALEANA Olney

Moist meadows at lower to medium elevations; rare.

Franklin Co.—*Svenson*, B. 9912, meadows on Elk River near Patterson Bridge, May 12, 1939 (determined by F. J. Hermann).

64. CAREX GRANULARIS Muhl.

Cedar glades, dolomitic slicks, meadows and stream banks at lower to medium elevations; fairly common.

Campbell Co.—*Underwood*, U. 147; Davidson Co.—*Svenson*, B. 10003; Knox Co.—*Underwood*, U.; Rutherford Co.—*Svenson*, B. 9078.

65. CAREX CRAWEI Dewey

Moist thin soils over calcareous rock; rare.

A. Gattinger reported it in cedar glades near Lavergne, Rutherford Co. K. K. Mackenzie also reports it in the state.

Section 18. Oligocarpae

66. CAREX OLIGOCARPA Schk.

Woods and thickets overlying limestone at lower to medium elevations; rare.

Cannon Co.—*Svenson*, B. 9266; Davidson Co.—*Gattinger**; Franklin Co.—*Svenson*, B. 10029; Hamilton Co.—*Churchill*, T., and *Sharp*, T. 957; Sumner Co.—*Weatherby*, T.

Section 19. Griseae

Pistillate spikes 3-15 flowered; bract-sheaths tight, not distinctly enlarged upward; leaf-blades light green or deep-green, not glaucous.
  Culms purplish-tinged at base; leaf-blades 2-4 mm. wide, erect; perigynia 3.5-4.5 mm. long; pistillate spikes widely separate, lower nearly basal ....67. *C. amphibola*
  Culms brownish-tinged at base; leaf-blades 4-7 mm. wide, ascending; perigynia

4.5-5.5 mm. long; lower pistillate spikes not nearly basal....................68. *C. grisea*
Pistillate spikes 10-45 flowered; bract-sheaths enlarged upward; leaf-blades glaucous (sometimes light-green in *C. flaccosperma*).
Perigynia 3-5 mm. long, somewhat exceeding the scales......................69. *C. glaucodea*
Perigynia 4.5-6 mm. long, 2-3 times exceeding the scales................70. *C. flaccosperma*

67. CAREX AMPHIBOLA Steud.

Woods, thickets and cedar glades mostly in calcareous soils at lower to medium elevations; infrequent. See Fig. 3 of plate.

Chetham Co.—*Svenson*, B. 7171 in part, 10206, 10352; Davidson Co.—*Svenson*, B. 9070; Giles Co.—*Svenson*, B. 8809; Loudon Co.—*Cain* and *Sharp*, T.; Knox Co. —*Underwood*, U. 4485; Montgomery Co.—*Svenson*, B. 9698; Morgan Co.—*Underwood*, U. 948; Rutherford Co.—*Freeman*, B. 14 and 301.

68. CAREX GRISEA Wahl.

Rich woods and thickets, at lower to medium elevations; infrequent.

Davidson Co.—*Gattinger**; Knox Co.—*Underwood*, U.; Loudon Co.—*Cain*, T.; Madison Co.—*Bain.**

69. CAREX GLAUCODEA Tuckerm.

Well drained rich woods and meadows mostly overlying limestone at lower to medium elevations; rare.

Davidson Co.—*Gattinger**; Franklin Co.—*Svenson*, B. 9310 and 10037.

70. CAREX FLACCOSPERMA Dewey

Meadows and shaded hillsides; rare.

To the author's knowledge there is no collection from Tennessee. K. K. Mackenzie does not report it in North American Flora from Tennessee. *Dr. A. Gattinger,** however, reported it near Nashville, Davidson Co. *H. K. Svenson* collected it over the State line in Jackson Co., Alabama, in a swamp.

Section 20. Gracillimae

Plants glabrous except that the lower sheaths are more or less hispidulous dorsally.
Perigynia beakless, rounded or short-tapering..71. *C. gracillima*
Perigynia beaked, the beak bent, nearly as long as the tapering and somewhat twisted body ....72. *C. prasina*
Sheaths, and often the leaf-blades, pubescent.
Terminal spike normally gynaecandrous; bracts sheathing at least lowest.
Perigynia 1.75-2.5 mm. wide, strongly nerved, the beak shallowly bidentate.
Upper scales of pistillate spikes acuminate or short-cuspidate; perigynia 3.5-4 mm. long, 1.75-2 mm. wide..73. *C. oxylepis*
Upper scales of pistillate spikes long-cuspidate; perigynia 4-5 mm. long, 2-2.5 mm. wide ....74. *C. Davisii*
Perigynia about 1 mm. wide, 2-ribbed and obscurely nerved, the orifice entire ....75. *C. aestivalis*
Terminal spike staminate; bracts sheathless...76. *C. misera*

71. CAREX GRACILLIMA Schw.

Rich, moist open woods, thickets and steep protected places at medium elevations; infrequent.

Cheatham Co.—*Svenson*, B. 10470; Cumberland Co.—*Sharp*, T. 3879; Davidson Co.—*Gattinger**; Sullivan Co.—*Underwood*, U. 1005(a).

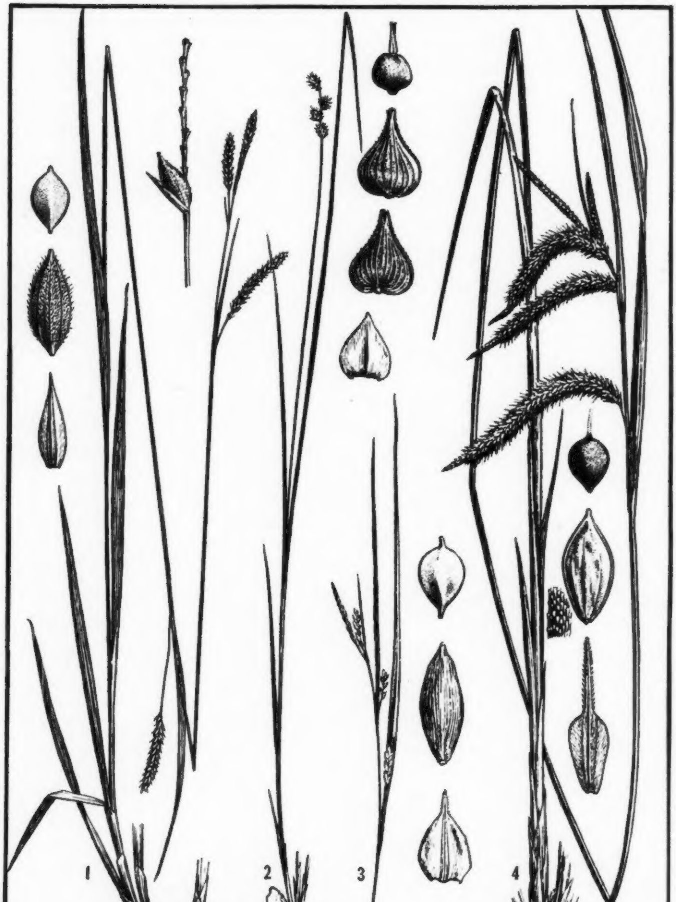


Fig. 1. *Carex oxylepis* var. *pubescens*, B. 10469. Habit ×1/2; fragment of spike showing rachis ×2½; perigynium, achene and scale ×5.

Fig. 2. *C. incomperta*, B. 10128 and B. 9325. Habit ×1/2; achene, perigynia (axial and abaxial faces) and scale ×5.

Fig. 3. *C. amphibola*, B. 10352. Upper part of culm ×1/2; achene, perigynium and scale ×5.

Fig. 4. *C. Mitchelliana*, B. 10448. Habit ×1/2; achene, perigynium and scale ×5; fragment of perigynium surface under magnification.

72. CAREX PRASINA Wahl.

Springy banks along shaded streams at medium elevations; infrequent.

Blount Co.—*Jennison*, T.; Cheatham Co.—*Svenson*, B. 7171 in part; Fentress Co.—*Underwood*, T.; Franklin Co.—*Svenson*, B. 10123; Hamilton Co.—*Gattinger**; Johnson Co.—*Underwood*, *Sharp*, U. 83; Lawrence Co.—*Svenson*, B. 9545; Lewis Co.—*Svenson*, B. 8799; Sullivan Co.—*Underwood*, U. 1005.

73. CAREX OXYLEPIS Torr. & Hook.

Woods overyling limestone and wooded bluffs at lower to medium elevations; rare.

Davidson Co.—*Svenson*, B. 9448; Franklin Co.—*Svenson*, B. 10039; Haywood Co.—*Bain*, N. Y. 493.

C. oxylepis var. **pubescens** var. nov. Similis speciei *Carex oxylepis* Torr. & Hook., nisi quod perigynia pubescentia et parvo graciliora: 3.5-4.0 mm x 1.25-1.75 mm. Achene quoque artior: 1.75-2.0 mm x 1.0-1.25 mm.

All collections were made by H. K. Svenson at the following stations: Cheatham Co., in oak-hickory woods on bluffs along Harpeth River near Pegram, May 6, 1939, *Svenson*, B. 10207 (Type, Herbarium Brooklyn Botanic Garden). See Fig. 1.

Pubescence has received too much attention as a species character. This is why this plant has not been raised to rank of a species.

74. CAREX DAVISII Schw. & Torr.

Alluvial woodlands mostly in calcareous soils at lower elevations; rare.

*A. Gattinger** reported it near Nashville, Davidson Co. *K. K. Mackenzie* reports it from Tennessee in North American Flora.

75. CAREX AESTIVALIS M. A. Curtis

Dry or moist mountain woods and meadows at medium to higher elevations; frequent.

Blount Co.—*Jennison*, T.; Cocke Co.—*Chickering*, T.; Cumberland Co.—*Underwood*, U. 2876; Fentress Co.—*Underwood*, U.; Putnam Co.—*Underwood*, U. 2985; Sevier Co.—*Underwood*, U. 121.

76. CAREX MISERA Buckley

Exposed rocky ledges on mountain summits and slopes; rare.

Carter Co.—*Underwood*, summit of Roan Mt., July 1931. Sevier Co.—*Underwood*, summit of Mt. LeConte, July 12, 1930. These are in the author's herbarium. Many other collections from Mt. LeConte and Clingman's Dome, Sevier Co., have been made since the fire and are in the University of Tennessee Herbarium.

Section 21. Sylvaticae

Achenes slenderly stipitate; perigynia glabrous; pistillate scales mostly obtuse.
  Perigynium 6-10 mm. long, 1.5-2 mm. wide, the beak 1.5-2 mm. long; scales white-hyaline-margined, rounded on back.......77. *C. debilis*
  Perigynium 4.5-7 mm. long, 1.75-2.25 mm. wide, the beak about 1 mm. long; scales tawny-tinged, sharply keeled.......78. *C. flexuosa*
Achenes sessile or nearly so; perigynium hirsutulous; pistillate scales cuspidate or awned.......79. *C. allegheniensis*

77. CAREX DEBILIS Michx.

Wet open woods, thickets and open swampy areas at lower to medium elevations; fairly common.

Bledsoe Co.—*Underwood*, and *Sharp*, U. 2992; Coffee Co.—*Svenson*, B. 7517 and 9151; Fentress Co.—*Svenson*, B. 9326; Franklin Co.—*Svenson*, B. 10140; Grundy Co.—*Svenson*, B. 8862; Lawrence Co.—*Svenson*, B. 9543a; Lewis Co.—*Svenson*, B. 8800; Marion Co.—*Svenson*, B. 8891; Morgan Co.—*Svenson*, B. 4091; Putnam Co.—*Svenson*, B. 10453, a collection with hirtellous margins of the perigynia and scale midrib is perhaps a transition to C. *allegenhiensis;* Sevier Co.—*Cain*, T.

According to H. K. Svenson who has seen the type of C. *debilis* in Paris, the lower perigynia are rather distant. It, more often than otherwise, shows scattered hirtellous projections on the margins of the beak, and very frequently on the surface of the perigynium under a good binocular. Number 10453 is an extreme case.

78. CAREX FLEXUOSA Muhl.

Mountain meadows, open well drained woods in acid soils at higher elevations in East Tennessee; common.

Bledsoe Co.—*Underwood*, *Sharp*, T.; Blount Co.—*Sharp*, T.; Carter Co.—*Underwood*, U.; Green Co.—*Jennison**; Johnson Co.—*Underwood*, *Sharp*, U. 31; Sevier Co.—*Underwood*, U. 2630.

79. CAREX ALLEGHENIENSIS Mackenzie

Open woodlands and bogs, mostly at medium elevations in mountains of East Tennessee; infrequent.

Bledsoe Co.—*Underwood* and *Sharp*, U. 2991; Blount Co.—*Jennison**; Cumberland Co.—*Svenson*, B. 4164; Fentress Co.—*Underwood*, U.; Johnson Co.—*Underwood* and *Sharp*, U. 32; Sevier Co.—*Jennison*, T.

Too much importance has been placed on pubescence as a species character. Perhaps this is a form of C. *debilis*. Fernald and Svenson are of this opinion since this plant is not well differentiated from C. *debilis*. Although C. *oblita* and C. *venusta* are not represented here this same relation of pubescence exists between them.

Section 22. Longirostres

80. CAREX CHEROKEENSIS Schw.

Swamps, woods, glades and banks of streams, at lower to medium elevations; infrequent eastward but fairly common in Middle Tennessee.

Davidson Co.—*Svenson*, B. 9067; Franklin Co.—*Svenson*, B. 10034, 10234; Rutherford Co.—*Freeman*, B. 22; Sevier Co.—*Svenson*, B. 7055.

Section 23. Virescentes

1. Perigynia densely pubescent, green; lower spikes more or less strongly distant and peduncled; ligule conspicuously longer than wide.
   2. Lowest bract setaceous, 0.5 mm. wide, twice exceeding inflorescence; pistillate spikes oblong-cylindric to oblong-globose; perigynia broadly obovoid; leaves usually exceeding culms; achenes bent apiculate; style as long as apiculation ....81. C. *Swanii*
   2. Lowest bract leaflet-like, 0.5-3 mm. wide, somewhat exceeding inflorescence; pistillate spikes linear-cylindric; perigynia oblong-elliptic or obovoid; culms exceeding leaves; achenes straight-apiculate; style much longer than apiculation ....82. C. *virescens*

1. Perigynia glabrous or at most asperulous (or with sparse pubescence when young); spikes contiguous or approximate or the lowest slightly remote, sessile or nearly so; ligule shorter than or about as long as wide.
   3. Perigynia more or less flattened ventrally, rounded at apex, nerved; achenes with a somewhat bent short-apiculate tip; style very short, not abruptly bent.
      4. Leaf-blades glabrate or nearly so, stiff, with revolute margines; perigynia somewhat flattened, very obscurely nerved or nerveless ventrally, more or less strongly nerved dorsally especially toward apex..............83. *C. complanata*
      4. Leaf-blades strongly short-pubescent, not stiff, flat; perigynia markedly flattened ventrally, strongly nerved dorsally, and less so ventrally....................................83. *C. hirsutella*
   3. Perigynia turgid, nearly round in cross-section, short pointed at apex, coarsely nerved or ribbed; achenes with a very abruptly bent apiculate tip or style.
      5. Perigynia 2 mm. long, brownish-green; pistillate scales not pilose, obtuse or short-cuspidate; leaf-blades glabrate with traces of pubescence....................................85. *C. caroliniana*
      5. Perigynia 2.5-3.5 mm. long, olive-green; pistillate scales sparingly pilose, cuspidate or awned; leaf-blades soft-pubescent, especially below....................................86. *C. Bushii*

81. CAREX SWANII (Fernald) Mackenzie

Well drained open woodlands and thickets, lower to medium elevations; frequent.

Blount Co.—*Underwood*, U.; *Wallace*, T.; Morgan Co.—*Underwood*, U. 943; Sevier Co.—*Sharp*, *Underwood*, T.

82. CAREX VIRESCENS Muhl.

Well drained open woods, slopes and bluffs, lower to medium elevations; frequent.

Anderson Co.—*Sharp*, T. 2744; Blount Co.—*Underwood*, U.; Cannon Co.—*Svenson*, B. 9288; Cheatham Co.—*Svenson*, B. 10348; Cocke Co.—*Sharp**; Davidson Co.—*Gattinger**; Franklin Co.—*Gattinger**; Hamilton Co.—*Lamson-Scribner**; Johnson Co.—*Underwood*, *Sharp*, U. 35; Knox Co.—*Lamson-Scribner**; Marion Co.—*Svenson*, B. 8900; Morgan Co.—*Svenson*, B. 9346, and *Underwood*, U. 967; Sevier Co.—*Underwood*, U. 142.

83. CAREX COMPLANATA Torr. & Hook.

Barrens and other woodlands at lower to medium elevations; infrequent.

Cheatham Co.—*Svenson*, B. 10347; Chester Co.—*Bain**; Coffee Co.—*Svenson*, B. 8719, 9171; Cumberland Co.—*Svenson*, B. 7466; Fentress Co.—*Underwood*, U. 2864; Franklin Co.—*Svenson*, B. 10217; Grainger Co.—*Sharp*, U.; Grundy Co.—*Svenson*, B. 7287; Knox Co.—*Lamson-Scribner**; *Underwood*, U.; Morgan Co.—*Svenson*, B. 8991; Sumner Co.—*Gattinger**; Wilson Co.—*Gattinger*.*

84. CAREX HIRSUTELLA Mackenzie

Barrens, other woodlands, thickets and meadows mostly in calcareous soils at lower to medium elevations; infrequent.

Bradley Co.—*Sharp*, T. 1087; Cheatham Co.—*Svenson*, B. 9026, 10339 and 10347 resembles *C. virescens* in many characters; Davidson Co.—*Svenson*, B. 9066; Franklin Co.—*Svenson*, B. 9692; Knox Co.—*Underwood*, U. 4482; Morgan Co.—*Underwood*, U. 940; Rutherford Co.—*Freeman*, B. 122; Sevier Co.—*Jennison*, T.; Union Co.—*Morrison*, T.

85. CAREX CAROLINIANA Schw.

Barrens, other woods and meadows at lower to medium elevations; infrequent.

Coffee Co.—*Svenson*, B. 7160; Cumberland Co.—*Svenson*, B. 4153; Grainger Co. —*Sharp*, T. 1598; Haywood Co.—*Bain*, N. Y. 491; Morgan Co.—*Underwood*, T.; Polk Co.—(probable), *Kearney*,* collected along Hiwassee River Valley; Sequatchie Co.—*Svenson*, B. 8753.

86. CAREX BUSHII Mackenzie

Dry meadows and banks in calcareous regions. A specimen tentatively named and collected by the writer in Knox Co., in 1930, was lost in the Morrill Hall fire. This species has been included not so much on the strength of a tentative identification, but more so because the state is within its range.

Section 24. Hirtae

87. CAREX LANUGINOSA Michx.

In low wheat fields; rare.

Madison Co.—*Bain* (probable collector), N. Y. 487, as *C. hirta* L.

Section 25. Anomalae

88. CAREX SCABRATA Schw.

Springy slopes in woodlands, thickets, and rocky stream beds at medium to higher elevations in the mountains of East Tennessee; infrequent.

Blount Co.—*Underwood*, U.; Johnson Co.—*Sharp*, *Underwood*, U. 62; Sevier Co.—*Underwood*, U. 139.

Section 26. Shortianae

89. CAREX SHORTIANA Dewey

Moist woodlands, thickets and meadows in calcareous districts; rare.

Davidson Co.—*Gattinger*,* at Tunnel Hill, Nashville; Knox Co.—*Kearney*, N. Y., moist meadows.

Section 27. Pendulinae

Perigynia strongly ribbed, often but slightly glaucous; pistillate scales not retuse; staminate scales tapering into the awn; basal sheaths not filamentose..........90. *C. Joorii*

Perigynia several-nerved, very glaucous; pistillate scales deeply retuse; staminate scales retuse; abruptly awned.

Pistillate spikes erect, the lower short peduncled; basal sheaths little if at all filamentose..........91. *C. verrucosa*

Pistillate spikes nodding at maturity, the lower long-peduncled; basal sheaths usually filamentose..........92. *C. glaucescens*

90. CAREX JOORII L. H. Bailey

Shallow water, open grassy swamps on Cumberland Plateau and in West Tennessee on hummocks in cypress swamps, lower to medium elevations; rare.

H. K. Svenson made the following collections:

Coffee Co.—B. 8763; Franklin Co.—B. 10405; Marion Co.—B. 9519; Sequatchie Co.—B. 9658.

Madison Co.—*Bain*.*

91. CAREX VERRUCOSA Muhl.

Pineland swamps at lower elevations; rare.

Collections made by S. M. Bain* in Chester and Madison Counties, 1892.

92. CAREX GLAUCESCENS Ell.

Open swamps and borders of ponds on Cumberland Plateau, at lower to medium elevations; rare.

Grundy Co.—*Svenson*, B. 8884 and 9183.

Both *C. Joorii* and *C. glaucescens* grow in the same type of habitat and look alike except that the perigynium in *C. Joorii* is more nerved and is less glaucous. Other differentiating characters such as differences in staminate scales and basal sheaths are not well defined.

Section 28. Limosae

93. CAREX BARRATTII Schw.

Swamps in oak barrens at lower to medium elevations; rare.

Coffee Co.—*Svenson*, B. 7519 and 10104.

Section 29. Acutae

Pistillate spikes erect; culms slender to base........94. *C. strictior*
Pistillate spikes at least the lower nodding or curved; culms stout below........95. *C. torta*

94. CAREX STRICTIOR Dewey

C. stricta var. *strictior* Carey.

Open swamps, roadside ditches in the higher elevations of East Tennessee; rare.

Underwood, Sharp, roadside bog, Shady Valley, Johnson Co., U. 1535, June 17, 1934.

95. CAREX TORTA Boott.

Rocky beds of streams, at medium to higher elevations in East Tennessee; infrequent.

Grundy Co.—*Svenson*, B. 7628; Marion Co.—*Svenson*, B. 10084; Monroe Co.—*Lamson-Scribner**; Morgan Co.—*Underwood*, U.; Polk Co.—(probable), *Ruth*,* in valley of the Hiwassee River; Sevier Co.—*Underwood*, U. and *Cain*, T.

Section 30. Cryptocarpae

Perigynia strongly papillate, slenderly few-nerved; achenes not constricted in the middle, suborbicular, the style straight; lower sheaths finely hispidulous dorsally; lower pistillate scales abruptly awned........96. *C. Mitchelliana*
Perigynia smooth or slightly granular, nerveless or faintly nerved; achenes abruptly constricted in the middle, oblong-ovoid, the style bent.
  Sheaths rough-hispidulous dorsally; lower pistillate scales tapering into the awn........97. *C. gynandra*
  Sheaths smooth dorsally; lower pistillate scales abruptly contracted into the awn and deeply retuse........98. *C. crinita*

96. CAREX MITCHELLIANA M. A. Curtis

Swamps of the lower Cumberland Plateau; rare. See Fig. 4 of plate.

Svenson, bog about 5 miles southeast of Sewanee, Marion Co., B. 8893, June 22, 1938; filling an open swamp north of Monterey Lake, Putnam Co., B. 10448, July 9, 1939.

C. mitchelliana grows in large clumps in shallow water of open swamps, sometimes in company with *C. crinita* which it closely resembles. These two species can be readily distinguished by the perigynia which are more or less appressed or ascending in *C. mitchelliana* and not divaricate as in *C. crinita.* In this respect it resembles *C. gynandra.*

97. CAREX GYNANDRA Schw.

Swampy or moist woodlands, at medium to higher elevations of East Tennessee; rare.

Sevier Co.—*Underwood*, U.; and *Cain*, T.; Washington Co.—*Sharp*, T.

98. CAREX CRINITA Lam.

Swamps, swampy woods and thickets from lower to medium elevations; common.

Fentress Co.—*Underwood*, U.; Grainger Co.—*Sharp*, T.; Grundy Co.—*Svenson*, B. 7295, and 8882; Johnson Co.—*Underwood* and *Sharp*, T.; Morgan Co.—*Underwood*, U. 936; Putnam Co.—*Svenson*, B. 6871 and 10449; Van Buren Co.—*Svenson*, B. 8741.

Section 31. Folliculatae

99. CAREX FOLLICULATA L.

Swampy woods in acid soils, at medium to higher elevations; rare.

Bledsoe Co.—*Underwood* and *Sharp*, U. 2987; Johnson Co.—*Underwood* and *Sharp*, U. 57.

Section 32. Pseudo-cypereae

Perigynia spreading or ascending, suborbicular in cross-section; ligule short, wider than long or about as wide as long; leaves 2-10 mm. wide.
- Staminate scales cuspidate or acute; pistillate scales with non-ciliate bodies; culms light-brownish-tinged at base .... 100. *C. Schweinitzii*
- Staminate scales with rough awns; pistillate scales with bodies ciliate-serrulate above; culms purple-tinged at base .... 101. *C. hystricina*

Perigynia reflexed, flattened-triangular in cross-section; ligule longer than wide; leaves 6-16 mm. wide .... 102. *C. comosa*

100. CAREX SCHWEINITZII Dewey

Swamps or springy banks in calcareous districts; rare.

Knox Co.—*Ruth*, N. Y. 870.

101. CAREX HYSTRICINA Muhl.

Swamps and wet meadows in calcareous districts; rare.

Collected by *A. Ruth** near Knoxville, Knox Co.

102. CAREX COMOSA Boott.

Swamps and non-acid soils. This species has not been collected within the State bounds to the writer's knowledge. It has been included between the State is within its range.

Section 33. Paludosae

103. CAREX HYALINOLEPIS Steud.

C. riparia var. *impressa* S. H. Wright.

Open swamps and wet swales in calcareous and non-acid soils; rare.

Madison Co.—near Jackson, *Bain*, N. Y. 488 (as *C. riparia*).

Section 34. Squarrosae

Scales equalling or exceeding perigynia; terminal spike usually small, 0.5-3 cm. long, normally staminate; ligule somewhat longer than wide to shorter than wide; perigynia strongly 12-20-ribbed; achenes 1.5 mm. long........104. *C. Frankii*

Scales much shorter than perigynia; terminal spike gynaecandrous; ligule much longer than wide; perigynia strongly several-ribbed above; achenes 2.5-3 mm. long.

Achenes linear-oval with flattish sides; style very strongly sinuous or abruptly bent below; spikes oval or oblong-oval, the perigynia with widely radiating beaks; pistillate scales acute to short-awned........105. *C. squarrosa*

Achenes obovoid with concave sides; style straight below; spikes oblong-cylindric, the perigynia with beaks mostly appressed-ascending; pistillate scales mostly obtusish........106. *C. typhina*

104. CAREX FRANKII Kunth.

Swamps, wet meadows in calcareous districts at lower to medium elevations; common.

Blount Co.—*Sharp*, T.; Davidson Co.—*Svenson*, B. 4201 and 9446; Grainger Co. —*Morrison*, T.; Knox Co.—*Underwood, Sharp*, T.; Marion Co.—*Sharp* and *Underwood*, U. 1124; Meigs Co.—*Underwood, Sharp*, U. 1042; Rutherford Co.—*Freeman*, B. 11; Sevier Co.—*Underwood*, U. 138; Union Co.—*Morrison*, T.

105. CAREX SQUARROSA L.

Swampy or wet woods, acid soils at lower to medium elevations; rare.

Davidson Co.—*Gattinger**; *Svenson*, B. 9443; Meigs Co.—*Underwood, Sharp*, U. 1038; Sevier Co.—*Jennison*, T. 2437.

106. CAREX TYPHINA Michx.

C. typhinoides Schw.

Rich alluvial woods and swamps; rare.

Coffee Co.—*Svenson*, B. 8761, at Sinking Pond south of Manchester, August 20, 1938.

Section 35. Vesicariae

Pistillate scales not rough awned.

Perigynia 3.5-8 mm. long, 2.5-3.5 mm. wide, strongly several-nerved, beak 1-2 mm. long, smooth; leaf-blades 2-12 mm. wide........107. *C. rostrata*

Perigyinia 7-9 mm. long, 2.5 mm. wide, strongly 10-ribbed, beak 3 mm. long, rough; leaf-blades 2-5 mm. wide........108. *C. bullata*

Pistillate scales with long rough awns.

Pistillate spikes cylindric to globose, 14-20 mm. wide; perigynia tapering or contracted into the beak, the beak shorter than the body; leaf-blades 2-7 mm. wide........109. *C. lurida*

Pistillate spikes narrowly oblong-cylindric, 8-13 mm. wide; perigynia abruptly contracted into the beak, the beak as long as or longer than the body; leaf-blades 2-4 mm. wide........110. *C. Baileyi*

107. CAREX ROSTRATA Stokes

Swamps and bogs of higher mountains of northeastern Tennessee; rare.

Johnson Co.—*Underwood*, and *Sharp*, U. 60, Shady Valley bog, 2800 ft. elevation, June 14, 1933.

108. CAREX BULLATA Schk.

Swampy meadows and acid soils at lower to medium elevations; rare.

Coffee Co.—*Svenson*, B. 9955; Davidson Co.—*Gattinger**; Franklin Co.—*Svenson*, 10138; Johnson Co.—*Underwood, Sharp*, U. 50.

109. Carex lurida Wahl.

Swamps and wet meadows from lower to higher elevations; common.

Anderson Co.—*Varnell*, T.; Blount Co.—*Jennison*, T.; Davidson Co.—*Gattinger**; Fentress Co.—*Underwood, Sharp*, T.; *Svenson*, B. 9326a; Grainger Co.—*Sharp*, T.; Hawkins Co.—*Underwood, Sharp*, T.; Knox Co.—*Underwood, Sharp*, T.; Lawrence Co.—*Svenson*, B. 9543; Lewis Co.—*Svenson*, B. 8797; Madison Co.—*Bain**; Marion Co.—*Underwood, Sharp*, T.; Monroe Co.—*Lamson-Scribner**; Putnam Co.—*Svenson*, B. 6872, 10450; Sevier Co.—*Cain*, T.; Sullivan Co.—*Underwood, Sharp*, U. 995; Washington Co.—*Sharp*, T.

110. Carex Baileyi Britton

Swampy meadows and woods in mountains of East Tennessee; rare.

Putnam Co.—*Underwood*, U. 2986, and Sullivan Co.—U. 87.

Section 36. Lupulinae

Pistillate spikes globose or subglobose; style normally straight; achenes sessile; perigynium-teeth hispid within; rootstocks very short, without long horizontal stolons.
- Perigynia cuneate at base and broadly stipitate, subcoriaceous, dull-green, usually more or less hispidulous; leaf-blades 4.5-14 (average 7-10) mm. wide; bract-sheaths not prolonged upward at mouth beyond base of blade; pistillate spikes 6-30-flowered.......111. *C. Grayii*
- Perigynia rounded at base, sessile or nearly so, membranous, shining, smooth; smooth; leaf-blades 2.5-9 (average 3-5) mm. wide; bract-sheaths short-prolonged upward at mouth beyond base of blade; pistillate spikes 1-15-flowered.......112. *C. intumescens*

Pistillate spikes oblong to cylindric; style abruptly bent; achenes broadly stipitate; perigynium-teeth smooth or nearly so within; stolons long, slender, horizontal.
- Achenes much longer than wide, the sides shallowly concave, the angles not prominently knobbed; pistillate spikes short-oblong to oblong cylindric.
  - Plants with culms arising 1-to-few together from elongate rootstocks; leaf-blades 2-6 mm. wide; pistillate scales acute to acuminate; bract-sheaths short-prolonged and convex at mouth.......113. *C. louisianica*
  - Plants cespitose; leaf-blades 4-16 mm. wide; pistillate scales acuminate to strongly aristate; bract-sheaths strongly prolonged and acutely high-convex at mouth.......114. *C. lupulina*
- Achenes about as wide as or wider than long, the sides deeply concave, the angles prominently knobbed; pistillate spikes cylindric or oblong-cylindric.
  - Perigynia ascending or somewhat spreading, the beak less than twice as long as the body; bract-sheaths strongly prolonged and acutely high-convex at mouth.......115. *C. lupuliformis*
- Perigynia widely spreading at maturity, the beak 1.5-3 times the length of the body; bract-sheaths short-prolonged and convex at mouth.......116. *C. gigantea*

111. Carex Grayii Carey

Rich alluvial woods and swamps in calcareous districts at lower to medium elevations; infrequent.

A. Gattinger reported this species in the swamps of West Tennessee.

Davidson Co.—*Svenson*, B. 9441; Hardin Co.—*Svenson*, B. 4326; Marion Co. —*Underwood, Sharp*, U. 1123, an hispidulous form.

112. Carex intumescens Rudge

Swampy or moist woods, acid soils at lower to higher elevations; a more slender variety (*S. intumescens* var. *Fernaldii* L. H. Bailey) apparently, is found only in the higher mountains in cool moist woods; frequent.

Blount Co.—*Underwood*, U. 4554; Coffee Co.—*Svenson*, B. 7518, 9150; Cumberland Co.—*Harbison*, T. 3079, and *Svenson*, B. 6913; Davidson Co.—*Gattinger**; Fentress Co.—*Underwood*, U.; 2900, and *Svenson*, B. 4110, 9323; Grainger Co.—*Underwood*, U.; Haywood Co.—*Bain**; Johnson Co.—*Underwood* and *Sharp*, U. 37; Marion Co.—*Svenson*, B. 8892; Morgan Co.—*Sharp* and *Underwood*, U. 2780; Putnam Co.—*Svenson*, B. 10456; Sevier Co.—*Underwood*, U. 246.

113. CAREX LOUISIANICA L. H .Bailey

Swampy woods and boggy meadows; rare.

Franklin Co.—*Svenson*, B. 9913, at Elk River near Patterson's Bridge, May 12, 1939.

114. CAREX LUPULINA Muhl.

Swamps in calcareous or neutral soils at lower to medium elevations; infrequent.

Blount Co.—*Greene*, T.; Cocke Co.—*Sharp*, T. 1090; Cumberland Co.—*Underwood*, U. 2913; Davidson Co.—*Gattinger*,* and *Walter Dean*, T. and *Svenson*, B. 7396; Grundy Co.—*Svenson*, B. 9114; Johnson Co.—*Underwood* and *Sharp*, U. 61; Knox Co.—*Ruth*, T.; Loudon Co.—*Sharp*, T. 1090; Marion Co.—*Underwood* and *Sharp*, U. 1093; Sumner Co.—*Svenson*, B. 7013.

115. CAREX LUPULIFORMIS Sartwell

A Gattinger reported it in the State. Several collections were tentatively labeled, but were finally placed as *C. lupulina*. The author has not seen good *C. lupuliformis* collected in this State. Svenson's No. 7396 issued as *C. lupuliformis* has achenes which are short and knobbed at the angles, as in characteristic illustrations of the species in Gray's New Manual, ed. 7, but the inflorescence is shortened and the achene surface has slightly convex cells as in *C. lupulina*. Whether such collections establish a transition between the two species has not been determined.

116. CAREX GIGANTEA Rudge

Swampy woodlands at lower and medium elevations; rare.

Coffee Co.—*Svenson*, B. 8781, 9409, 10266; Grundy Co.—*Svenson*, B. 10146; Marion Co.—*Svenson*, B. 9317. *Lamson-Scribner** at White Cliff Springs, July 5, 1890, county unknown to the author.

The North American Species of Smilacina

Desma H. Galway

Introduction

This paper is the result of a taxonomic study of the species of the genus *Smilacina* occurring naturally in North America north of Mexico. In the past it has been difficult to make satisfactory determinations of members of this genus from existing manuals, especially among western forms. West of the great plains the great diversity in environmental conditions has given rise to a diversity in form of the species that are widely distributed. Many of these forms have been given specific or varietal names recently, and as no comprehensive work on the genus has been done since most of these were published, it is hoped that this study will be generally helpful in identifying members of the group.

During the preparation of this work over 2500 herbarium specimens have been examined and annotated and comparative measurements made of many of these. These include either the types or specimens designated by the author of the name as typical of nearly all of the forms for which names have been published.

Specimens have been examined from all of the forty-eight states except Louisiana and Florida, also from Canada, Alaska, Mexico, Central America, and Asia. Field work has been comparatively limited. However, specific differences in the genus *Smilacina* have been based mostly on gross morphological characters, readily discernible in herbarium material.

History

The species now assigned to the genus "Smilacina" have been subject to considerable controversy, and in all have been published under at least thirteen different generic names.

In his *Species Plantarum* (17, p. 315), in 1753, Linnaeus published the genus *Convallaria* which included three species now referred to *Smilacina*, and species of *Maianthemum, Polygonatum,* and *Convallaria* proper.

In 1763 Adanson published *Vagnera* in honor of Richard Wagner, without, however, citing species. From his description the application of the name is evident, and his was the first attempt to split Linnaeus' *Convallaria* into more natural, smaller groups. However his work was not given recognition at that time.

In 1790 Necker published *Tovaria,* citing to it the three Linnaean species later included in Desfontaine's *Smilacina*. However he did not publish species names as such, and his generic description was inaccurate (See Victorin, 30, p. 80), so that his work has not generally been credited. Later Ruiz and Pavon published the name *Tovaria* for a South American genus related to the *Cap-*

paridaceae, and the name is now held valid for that group. In 1763 Adanson published the distinct name *Tovara* for a genus in the *Polygonaceae.*

In 1807 Desfontaines published the name *Smilacina* (the name meaning Smilax-like). His generic description was brief but accurate. He included in the genus Linnaeus' three species, also the present *Clintonia umbellata,* based on Michaux's *Convallaria umbellata* (Fl. Boreal. Amer. 1, p. 202), and a fourth member similar to *Smilacina amplexicaulis* which he called *S. ciliata.*

During the fore part of the nineteenth century, botanical exploration in Central America and Asia brought to light a number of other affiliated species. In 1850, Kunth divided the expanded genus into three genera, which he named *Asteranthemum, Jocaste,* and *Medora.* Occasionally specimens of North American forms are still found in herbaria labeled as *Asteranthemum.*

In 1821 Link published *S. racemosa* and *S. stellata* under *Maianthemum* of Wiggam. This name is now confined to a closely related genus, distinguished from *Smilacina* by the 2- rather than 3-merous flowers.

In 1794 Moench published *Polygonastrum;* in 1819 Rafinesque published *Sigillaria* and *Styrandra;* in 1866 Salisbury published *Neolexis;* all names of questionable application and all but *Polygonastrum* antedated by *Smilacina.*

In 1875 Baker revived *Tovaria* of Necker and republished all the species he recognized under this name. In 1888 and 1889 Greene and Britton republished the species then known, at least as to North American forms, under *Unifolium,* including them with *U. bifolium.* Referring to Desfontaine's original publication of *Smilacina,* Greene regarded *S. umbellata* as the type species of the genus, and hence referred the species of *Clintonia* to *Smilacina.*

In 1894 Morong brought to light Adanson's publication of *Vagnera* and republished all of the North American species under this name. *Vagnera* was held as the accepted name of the genus by proponents of the "American Code" from that time on. In 1905, however, *Smilacina* was placed on the list of *nomina conservanda* by the Vienna Congress on the basis of long usage.

During the latter part of the 19th century, Nuttall (published by Baker), Greene, and Rydberg proposed several new species, mainly from western North America. Since the beginning of this century taxonomic work on the North American species has been confined to the naming of a few new varieties and forms. These will be discussed in detail later.

Economic Importance

Smilacina racemosa and *S. stellata,* also *S. paniculata* of Mexico and Central America, are occasionally cultivated for ornamental use because of their graceful habit, attractive, bright green foliage, and clusters of flowers and fruit.

None of the species have any forage value although they are not known to contain any poisonous principle. The "Palatability Tables for Region 4" in the Western United States, compiled by the U. S. Forest Service, list the palatability of "*Vagnera*" species as "5," a very low rating. In certain areas in New Mexico and perhaps elsewhere, increases in abundance of *Smilacina*

stellata is regarded as evidence of overgrazing. (See Sampson, 26, pp. 36-37, 39.)

The berries are not agreeable in flavor to man, although they appear to be eaten by certain birds. Those of *S. trifolia* are said to contain an active cathartic and were used as such by early explorers in subarctic regions. (See Victorin, 30, p. 86.)

That the West Coast Indians found a use for the plant is indicated by the following note taken from a herbarium sheet of *S. stellata* belonging to the Field Museum. The plant was collected in California "Near Monolith, Piute Mts., Kern Co. Maurice L. Zigmond 104, July 7, 1937. 4400-5500 ft.

"Pa'ro'ra ba. Plant growing by water. Has green berries striped purple. Root is mashed and put in stream to stun fish. Fish float to top of water and are caught in yadaci (winnower), thrown to bank."

Evolution and Relationships

Smilacina is a member of the tribe *Polygonatae* in the family *Liliaceae*. (See Hutchinson ,14, p. 94.) The tribe is characterized by having an underground rhizome and a leafy aerial stem, also by the fruit, which is always a berry. *Smilacina* is distinguished from the other genera of the tribe by its simple aerial stem bearing several alternate leaves; its single, terminal inflorescence which may be either racemose or paniculate; and its six distinct perianth segments. Our species have white or greenish white flowers. The flowers of some Central American and Asiatic species are rose, purple, or cream-colored.

The nearest relative of *Smilacina* is probably *Maianthemum*, which was perhaps derived from the former genus by a reduction in the number of flower parts from six to four. *Disporum*, with branching stem and few-flowered, terminal inflorescence, also appears to be closely related.

Smilacina is considered as primitive in having distinct perianth-segments and a many-flowered inflorescence. It is advanced in its simple stem and single, terminal inflorescence. The most primitive of *Smilacina* species is probably *S. racemosa*, as evidenced by its wide distribution near the geographic center of the range of the genus and its unspecialized, paniculate inflorescence. Other species seem to have arisen in the four following ways: 1, the development of a more vigorous habit of growth (mainly tropical forms, *S. paniculata, S. thyrsoidea*); 2, the development of pigmented flowers (*S. Japonica, S. Salvinii*); 3, the reduction of the inflorescence from a panicle to a simple raceme (*S. stellata, S. trifolia*); 4, the adaptation to specialized environments (*S. trifolia* in peat bogs, *S. Salvinii* as an epiphyte).

It is interesting to trace among specimens still in existence the process whereby the paniculate inflorescence may have developed into the racemose type. In *S. racemosa*, the upper branches of the panicle frequently have the branch axis so shortened that the flowers appear to spring in an umbelliform cluster from the main axis. Specimens are occasionally seen, mostly from the South Central United States (New Mexico to Georgia), which have all branches so shortened. (Such a form was the type of Greene's *S. glomerata* ined.)

In S. flexuosa of Central America is found a similar condition; the inflorescence is "racemose," but several pedicels arise from each node of the axis, or at least from some of them. In this species, the pedicels are very long and the flowers much larger than in *S. racemosa;* consequently there is no danger of confusing the two species. *S. flexuosa* probably arose directly from a form like *S. paniculata,* another Central American form, which except for its long pedicels and general robust habit is similar to typical *S. racemosa.*

In *S. dahurica* of eastern Asia only a few of the nodes of the inflorescence bear more than one flower. In our *S. stellata,* this condition reaches its ultimate development, the inflorescence being strictly racemose. Even in this species, however, an occasional specimen is encountered bearing two flowers at one or more of the lower nodes.

S. Japonica, of southeastern Asia and Japan, and perhaps other species also, may have the inflorescence either branched or simple. Thus it will be seen that in the genus *Smilacina,* the terms "racemose" and "paniculate" may be only relative in their application to the description of the inflorescence, and cannot always be relied upon as a positive means of identifying species.

S. trifolia of subarctic regions in North America and Siberia is probably a reduced offshoot from *S. stellata.* It is distinguished by its lower stature, fewer leaves, and specialized habitat, being found only in cold, acid bogs.

Taxonomy

SMILACINA

Herbaceous perennials from creeping, scaly rootstocks; aerial stems simple, leafy; leaves alternate, simple, entire, lanceolate to ovate or cordate, sessile or petioled; inflorescence terminal, racemose or paniculate; perianth-segments distinct, 6; stamens 6, borne at the base of the perianth-segments; anthers versatile, dehiscing inwardly; ovary 3-celled; styles 3, distinct or united; ovules 2 in each cell of the ovary; fruit a round or 3-lobed berry, 1-6-seeded.

About 23 species, only 2 of which are confined to temperate North America and a third is found in both North America and Northern Siberia. Of the remainder, 7 are in Mexico and Central America, 8 in Eastern Asia and Japan, 4 in the Himalayan Region, and 1 in Arabia.

Plants mostly of moist soil in woodlands. Some tropical American species are epiphytic.

Citation of Specimens

No attempt has been made to cite collections showing complete distribution of each form. This is shown on the accompanying distribution maps. Rather it has been the aim to select some of the more interesting specimens, including "types" and unusual forms. Also included are a wide range of representative forms which were used in the biometrical studies.

The herbaria containing the cited specimens are designated by the following key:

Brigham Young University, Provo, Utah, "BY"
Field Museum of Natural History, Chicago, "FM"
Gray Herbarium of Harvard University, Cambridge, Mass., "GH"
Missouri Botanical Garden, St. Louis, Mo., "MBG"

University of Montreal, Montreal, Quebec, "UM"
Herbarium of Marie-Victorin, Montreal, Quebec, "MV"
New York Botanical Garden, "NY"
Herbarium of Pomona College, Claremont, Calif., "PC"
U. S. National Herbarium, Washington, D. C., "US"
Rocky Mountain Herbarium, Laramie, Wyoming, "RM."

KEY TO NORTH AMERICAN SPECIES

Inflorescence paniculate.
  Leaves abruptly long-acuminate, distinctly petioled, spreading.................1. *S. racemosa*
  Leaves merely acute or very short-acuminate, usually somewhat clasping by the sessile or wing-petioled base, usually ascending..1a. *S. racemosa* var. *amplexicaulis*

Inflorescence racemose.
  Leaves more than 4, sessile and abruptly narrowed at the base.
    Leaves not fleshy; plants of moist soil in open woodlands......................2. *S. stellata*
    Leaves fleshy; plants maritime, of marshy areas..................2a. *S. stellata* var. *crassa*
  Leaves 2-4, tapering gradually to the somewhat sheathing base..................3. *S. trifolia*

1. SMILACINA RACEMOSA (L.) Desf. Ann. Mus. Paris 9:53. 1807

Rootstock stout; stem erect, arcuate or spreading, usually puberulent at least in inflorescence, more or less flexuous, 30-70 cm. high; leaves lanceolate to elliptic, usually broadest at the middle, long acuminate or tailed at the apex, distinctly petioled and spreading, distichous, 2-7 cm. wide, 6-18 cm. long, distinctly veined, usually puberulent; inflorescence many-flowered, 3-13 cm. long, 1-8 cm. broad, with 5-20 branches; perianth-segments white or greenish, 1-2 mm. long, about .5 mm. wide; stamens exceeding the perianth segments, 1.5-3 mm. long, the anthers yellow, the filaments more or less inflated; style .3-1 mm. long; ovary .7-1.5 mm. long; berry globose, about 5 mm. in diameter, at first mottled red and green, later turning red or occasionally purple throughout.

Frequent in shady woods and forests in fairly moist soil throughout southern Canada and the United States, with the probable exception of Florida, Louisiana, and certain states of the intermountain West. In the latter region it is largely replaced by the variety *amplexicaulis*. It is absent in the plains region except along watercourses, and in the desert regions of the west is found only in the mountains. It is also found in the mountains of Chihuahua and in southern Alaska. (Fig. 1.)

This species is very variable in the size, shape, and surface texture of all its parts and has consequently been divided into a number of species and varieties. Only one of these has been retained. This conclusion was reached after making first a series of preliminary observations, comparing 35 specimens, including the types of most of the doubtful forms, comparing them on 36 characters which had or might have been cited to indicate specific or varietal differences. Those characters which from this comparison appeared significant, or which had been most stressed in literature, were then compared in large series of specimens. Among these may be mentioned leaf shape; length of petals, style, and peduncles; and shape, size, and density of inflorescence. The results of these studies are discussed later.

Doubt as to the validity of many of the named forms has been expressed by other authors. (See St. John, 25, pp. 95-97.) Index Kewensis, which does not list varieties, does not recognize any of the species.

Convallaria racemosa L. Sp. Pl. 315. 1753.
Tovaria racemosa Neck. Elem. **3**:190. 1790. (Name only) Based on *C. racemosa* L.
Maianthemum racemosum Link, Enum. pl. Hort. Berol. **1**:343. 1821. Based on *C. racemosa* L.

Fig. 1.—• Distribution of *Smilacina racemosa* (L.) *Desf.*
× Distribution of *Smilacina racemosa* (L.) Desf. var. *amplexicaulis* (Nutt.) S. Wats.
○ Distribution of intergrading forms of *Smilacina racemosa* and vaı. *amplexicaulis*.

Unifolium racemosum Britton, Trans. N. Y. Acad. Sci. **8**:74. 1889. Based on *C. racemosa* L.

Vagnera racemosa Morong, Mem. Torr. Bot. Club **5**:114. 1894. Based on *C. racemosa* L.

Smilacina racemosa (L.) Desf. var. *typica* Fernald, Rhodora, **40**:407. pl. 512. 1938.

Smilacina ciliata Desf. Ann. Mus. Paris **9**:53. 1807.

Vagnera brachypetala Rydb. Bull. Torrey Club **28**:268. 1901, as to type specimen.

Vagnera australis Rydb. in Small, Fl. S. E. U. S. 270, 1328. 1903.

Smilacina racemosa forma foliosa Victorin, Contrib. Lab. Bot. Univ. Montreal, **14**:15. fig. 1. 1929.

Smilacina racemosa (L.)Desf. var. *cylindrata* Fernald, Rhodora **40**:406. 1938.

Fig. 2.—• Distribution of *Smilacina stellata* (L.) Desf.
× Distribution of *Smilacina stellata* (L.) Desf. var. *crassa* Victorin.
○ Distribution of *Smilacina trifolia* (L.) Desf.

The basis for elimination of each of the synonyms as distinct species or varieties follows:

Smilacina ciliata Desf. In his description, Desfontaines, although he states that this species is "tres distincte" gives no characters which would serve to distinguish it from typical *S. racemosa*. The height of this species is described as only 3-6 cm., but this is probably a typographical error, dm. being meant rather than cm.

The illustration shows an abnormally bifurcate and trifurcate panicle, and since this condition is not found in nature in the genus, it is generally believed to be an interpolation by the artist. It is also believed that this species was founded upon a cultivated form which may have differed considerably in appearance from the wild plant, and which now may no longer be in existence. (See Fernald, 8, pp. 404-407.)

Vagnera brachypetala Rydb. Rydberg describes this species as having unusually short petals and purple, rather than typically red fruits. Of the five specimens he cites as representative, only one, the type, is in fruit. It is impossible to determine the length of the petals on this specimen. It has the long-petioled, long-acuminate leaves of typical *S. racemosa*.

Of the other four, the perianth segments range from about 1 to 1.5 mm. in length (the range of the species is 1-2 mm.), and the leaves of one are nearer the var. ampexicaulis. None of the specimens mentioned in the original description were collected by Rydberg, nor does he mention having seen the plant in the field.

Other herbarium specimens which have been referred to this species range from extreme *amplexicaulis* to typical *racemosa*, and have perianth-segments from 1 to as much as 2 mm. long. Few of them are fruiting, and in these, the herbarium specimen may appear to be either red or purple.

As the color of the fruit may depend upon the degree of maturity of the plant and the pH of the soil in which it is grown, however, it alone can hardly be regarded as a specific or even varietal character. It is also impossible to tell with certainty the color of the fruit from a herbarium specimen.

Vagnera australis Rydb. Rydberg based this species on 3 herbarium specimens in the New York Botanical Garden collected in Alabama and Georgia. He lists as key characters the following:

"Sepals and petals narrowly linear: filaments flat, twice as long as the perianth .... *V. australis*

"Sepals and petals broadly linear: filaments inflated, about as long as the perianth .... *V. racemosa*"

He also describes *V. australis* as being more slender and having relatively narrower leaf blades.

The perianth-segments on the cited specimens measure about .3 mm. in width, as compared with the average of .5 mm. for the species. The anthers also appear to be less inflated, and the plants are smaller than average specimens, the stems especially being slender (1.5-3 mm. as compared with the

average of 5 mm.). The other characters which Rydberg mentions as being distinctive—relative length of filaments and petals and relative width of leaves—are found to be about the same on the *V. australis* specimens as the average for the group. Other specimens collected at the type locality appear typical of *S. racemosa.*

The only basis for a new species or variety seems to lie in the size of some of the parts, in which there is wide variation and complete intergradation with the typical form of the species. For further discussion of the status of *V. australis*, see the treament of *S. racemosa* var. *cylindrata,* below.

Smilacina racemosa forma *foliosa* Victorin. Throughout the range of the species is found sporadically a form which has inflorescence sessile in the axil of the uppermost leaf. This is usually found in large, vigorous specimens and probably results from the development of the bractlet subtending the lowermost branch of the panicle into a leaflike structure. Rarely one or two bracts within the panicle are also enlarged. This development is also met with occasionally in the var. *amplexicaulis.*

Smilacina racemosa (L.) Desf. var. *cylindrata* Fernald. Fernald divided the bulk of the species into two varieties, a northern and a southern form, based on the relative vigor of the plants, size and shape of the panicle, and length of the peduncle. His summary of the distinguishing characters follows:

"NORTHERN SERIES. Stem up to 1 m. high; larger leaves of mature plants 1-2.5 dm. long, 3.5-9.5 cm. broad; panicle sessile or on a peduncle usually less than ½ its length, ovoid to pyramidal, 0.7-1.7 dm. long, 3-10 cm. in diameter, ⅜-¾ as broad as long, its longer branches 2-6 cm. long and with 8-24 flowers." = var. *typica.*

"SOUTHERN SERIES. Stem rarely 7.5 dm. high; larger leaves of mature plants 0.85-1.7 dm. long, 3.5-6 cm. broad; peduncle ½-1¼ as long as the nearly cylindric panicle; the latter 4.5-8.5 (rarely 13) cm. long, 1.5-3 cm. in diameter, ¼-⅜ as broad as long, its longest branches 1-2.5 cm. long, 6-10 flowered." = var. *cylindrata.*

He lists the range of both varieties by states, and says that in the region in which the ranges overlap, transitional forms are frequent.

The following table was constructed as a result of the examination and measurement of 168 specimens in the herbarium of the Missouri Botanical Garden, with reference to these characters cited by Fernald, and also those mentioned by Rydberg in describing *Vagnera australis,* included because it would be considered an extreme form of Fernald's var. *cylindrata,* the name he gives to the southern series, except for the rather short peduncle on the type specimen.

States listed under the heading "Northern Series" are those in which, according to Fernald, only var. *typica* is found; according to the same author, var. *cylindrata* is confined to the states listed under "Southern Series," while in the "Transitional" series intergrading occurs.

Examination of this table does reveal a tendency for plants in the northern portion of the range to average somewhat more vigorous habit of growth than those in the southern portion. However even allowing for the possibility that Fernald's statement as to geographical distribution might not be entirely accu-

TABLE 1.—Distribution of 3 named forms of *Smilacina racemosa*, with intergrades.

	typica	*typ-cyl* intergrade	*cylindrata*	*cyl-aus* intergrade	*australis*	Total
Northern series						
Alaska	1	..	1	..	..	1
Alberta*	..	..	1	..	..	1
British Columbia*	..	2	..	..	..	2
California*	2	1	2	..	..	5
Colorado*	..	..	2	..	..	2
Maine	..	..	2	..	..	2
Minnesota	2	1	..	..	..	3
New Brunswick	1	..	..	..	..	1
N. Dakota	1	1	..	..	..	2
Oregon*	3	..	1	..	..	4
S. Dakota	..	..	1	..	..	1
Vermont	3	3	1	..	..	7
Washington*	..	2	3	..	..	5
Wisconsin	..	..	..	1	..	1
Wyoming*	3	..	..	..	..	3
Total	16	10	13	1	..	40
Transitional						
Arizona*	..	..	..	..	1	1
Connecticut	1	1	..	..	..	2
Delaware	..	1	..	..	..	1
Dist. of Columbia	..	1	..	..	..	1
Illinois	3	3	2	..	..	8
Indiana	1	..	..	..	..	1
Iowa	1	1	3	..	..	5
Kansas	..	1	..	..	..	1
Kentucky	..	4	..	1	1	6
Massachusetts	1	1	1	..	1	4
Michigan	4	..	1	..	..	5
Missouri	8	6	16	3	4	37
New Hampshire	2	1	..	..	..	3
New Jersey	..	..	1	..	1	2
New York	3	..	..	1	..	4
Ohio	1	1	1			3
Pennsylvania	..	4	3	2	..	9
Rhode Island	..	..	1	..	..	1
Tennessee	..	..	..	..	1	1
Virginia	..	..	..	2	..	2
West Virginia	2	..	2	..	..	4
Total	27	25	31	9	9	101
Southern series						
Alabama	..	..	..	1	..	1
Arkansas	2	1	1	1	1	6
Georgia	..	..	1	..	4	5
Mississippi	..	..	..	..	1	1
North Carolina	..	1	..	1	..	2
New Mexico	3	..	..	..	..	3
Oklahoma	1	..	..	1	..	2
South Carolina	1	..	..	1	4	6
Texas	1	..	..	..	..	1
Total	8	2	2	5	10	27

* States in which var. *amplexicaulis* is also present.

rate, the statistics do not seem to warrant retaining either his var. *cylindrata* or Rydberg's *Vagnera australis*. This tendency for larger size of plants as one progresses northward along the range is found in many species of plants in the United States.

SELECTED SPECIMENS

ALABAMA: Auburn, April 22, 1896, Earle & Underwood (NY).

ALASKA: Alaskan Boundary Survey, Wrangell, (US 423091); River Road above Hyder, June 18, 1924, Kirk Whited 1222, (MBG 925546).

ARIZONA: Mt. Lemmon, July 28, 1926, Peebles, Harrison & Kearney 2517, (MBG 965354).

ARKANSAS: Five miles East of Mt. Ida on Highway 270, Garland Co., just off road in sandy soil, April 27, 1935, Maude C. Lodewyks 165, (MBG 1095075); Savoy, Washington Co., April 20, 1927, D. Demaree 3017, (MBG 960742).

BRITISH COLUMBIA: Glacier at the "Loup," August, 1897, Mr. and Mrs. Cornelius Van Brunt, (type of *V. brachypetala* Rydb.), (NY); Victoria, Vancouver Island, May 31, 1893, John Macoun 5998, (paratype of *V. brachypetala* Rydb.), (NY); Deer Park, Columbia River, June 6, 1890, John Macoun (paratype of *V. brachypetala* Rydb.), (NY); Prince George, June 30, 1935, O. J. Murie 1291, (MBG 1105542).

CALIFORNIA: Tamalpais, April 13, 1913, E. O. Wootton, (US 663951); Hems Station, Amador Co., 5000 ft., 1895, Geo. Hansen 1076, (MBG 147029).

COLORADO: S. E. of Ouray, chaparral covered hills, 2300-2600 meters, Sept. 7, 1901, M. L. Underwood & A. D. Selby 79, (This was the only specimen seen from Colorado, the leaves were long and narrow, shortly but distinctly petioled), (NY).

CONNECTICUT: Storrs, May 8, 1907, (inflorescence sessile), (MBG 792128).

DELAWARE: Tidestrom 7913, (MBG 806800).

DISTRICT OF COLUMBIA: (MBG 147054).

GEORGIA: De Kalle Co., Steene Mt., May 20, 1897, H. Eggert (MBG 147012); Yellow River, Gneime Co., July 27, 1897, H. Eggert, (MBG 147013); Rome, Dr. Ravenel, (MBG 147065).

ILLINOIS: Bellville, July 3, 1891, E. Douglas, (MBG 147005); Richland Co., May 16, 1922, R. Ridgway 1595, (MBG 916691).

INDIANA: Osborne, August 28, 1909, Greenman 2839, (MBG 738629).

IOWA: Bentonsport, Rich Woods, June 1920, E. W. Graves 1796, (MBG 975281); Decatur Co., Rich woods, May 23, 1898, J. T. Fitzpatrick, (MBG 147018); Iowa Lake, Emmett Co., June 1899, R. I. Cratty, (MBG 147003).

KANSAS: Cherokee Co., Rich woods, 1896, A. S. Hitchcock 835, (MBG 147033).

KENTUCKY: Natural Bridge, May 26, 1923, F. F. McFarland 69, (MBG 904091); Pine Mt., Bell Co., Sept. 1893, T. H. Kearney Jr. 348, (MBG 147045); Hopkinsville, May 26, 1920, Palmer 17655, (MBG 861596).

MAINE: Orono, Penobscot Co. & River, Rocky, open woods, July 26, 1895, Fernald 342 (MBG 147017); Washington, Knox Co., Moist, rich woods, August 24, 1929, Steyermark 882, (MBG 1026026).

MASSACHUSETTS: Concord, May 30, 1896, Greenman 2292, (this resembles very much the type of *V. australis* Rydb., supposedly a strictly southern form), (MBG 147074); Mongut, June 19, 1888, E. L. Sturvetantii (MBG 147074); Tynsboro, May 26, 1929; Fred'k S. Beattie, (BY).

MICHIGAN: Douglas Lake, Emmet Co., in aspens, F. C ~~D.~~ & M. T. Gates 10263, (MBG 823299); Cheboygan Co., F. C. & M. T. Gates 10514; (MBG 823897).

MINNESOTA: E. Shore Lake Josephine, Hubbard Co., July 16, 1933, J. B. Moyle 862, (MBG 1078018); Mankato River, June, 1818, C. C. Parry, (MBG 147057).

MISSISSIPPI: Tchula, April 18, 1927, R. E. Woodson & E. S. Anderson 1529, (MBG 934634).

MISSOURI: Eureka, May 18, 1901; J. H. Kellogg, (MBG 910145); Creve Coeur Lake, June 26, 1905, A. G. Johnson, (MBG 147044); Dodson, Jackson Co., Rich Woods, May 26, 1917, R. Hoffman (MBG 857806); St. Louis, July 26, 1890; Hitchcock, (MBG 147032).

NEW BRUNSWICK: Lily Lake, July 22, 1877, J. Fowler, (MBG 147020).

NEW HAMPSHIRE: Mt. Kearsage, White Mts., North Conway, June 10, 1874, Morong, (MBG 147051); Crawford Notch, July 3, 1898, Greenman 1128, (MBG 722195).

NEW JERSEY: Summit Co., R. Perry 32, (MBG 147059).

NEW MEXICO: Alamo National Forest, Haynes Canyon, in poplar thickets, August 10, 1911, Bronson Barlow, (MBG 146923).

NEW YORK: Ithaca, May 31, 1891, H. S. Schrenk, (MBG 147080).

NORTH CAROLINA: Biltmore, May 29, 1897, (MBG 146991); Chapel Hill, dry woods, May 11, 1928, Edgar Anderson, (MBG 942593).

NORTH DAKOTA: Fargo, rich soil, woods, July 21, 1912, H. F. Bergman, (MBG 743403).

NOVA SCOTIA: New Germany, June, 1891, Dr. Chas. A. Hamilton, (NY).

OHIO: Greenman 1258, (MBG 722193).

OKLAHOMA: Page, Rich woods, hillside, July 27, 1917, Palmer 12646, (MBG 828965).

OREGON: Multnomah Falls, May 30, 1899, T. H. Kearney Jr. & Coville 263, (US 373356); Corvallis, May 24, 1922, C. C. Epling 5096, (MBG 965206); Sykes Creek, Jackson Co.,May 26, 1892, E. W. Hammond 380, (MBG 86815).

PENNSYLVANIA: Mt. Alto, June 6, 1908, Jos. Illick, (MBG 147038); Mt. Ville, May 1891, Eby, (MBG 147008).

RHODE ISLAND: Greenman 1835, (MBG 722435).

SOUTH CAROLINA: Anderson, July 15, 1919, Rev. John Davis 8411, (MBG 855304).

SOUTH DAKOTA: Lead, Hillside, June 24, 1928, H. E. Lee (MBG 1078686); L. Oakwood, Griffiths, Thos. A. Williams, (MBG 147028).

TENNESSEE: Knoxville, May 18, 1898, Albert Ruth 151, (MBG 147070).

TEXAS: Davis Mts., Jeff Davis Co., Oct. 4, 1926, E. J. Palmer 31960, (this is an unusually large specimen, having pedicels up to 3 mm. long, seeds 4 mm. broad), (MBG 961690).

VERA CRUZ: Canton Cordoba, Cerro de Choraman, im nassigen Bergwaldern, May 12, 1907, Caec. et Ed Seler. 5174, (US 1206028).

VERMONT: Fairlee, Palisades, July 16, 1927, M. Mathias 145, (MBG 940334); Brandon, rich woods, June 5, 1922, D. L. Ditton, (MBG 915059); Peacham, August 6, 1885, F. Blanchard, (MBG 750369).

VIRGINIA: Little Neck, Princess Anne Co., dry mixed woods, August 8 and 9, 1934, Fernald & Long 3859, (type of *S. racemosa* var. *cylindrata* Fernald), (GH); Luray, Stony Man Mt. Blue Ridge, 3500 ft., August 31, 1901, Mr. & Mrs. E. S. Steele, (MBG 147073).

WASHINGTON: Seattle, May 21, 1891, C. V. Piper 198, (paratype of *V. brachypetala* Rydb.), (NY); Olympic Mts. Clallam, June, 1900, A. D. E. Elmer 2500, (MBG 146933).

WEST VIRGINIA: Buckhorn, Upshur Co., May 17, 1895, W. M. Pollock, (MBG 147060); Davenport, Tyler Co., June 21, 1930, E. E. Berkeley 764, (MBG 994193).

WISCONSIN: Ephraim, June 5, 1907, J. M. Greenman 3168, (MBG 740328).

1a. SMILACINA RACEMOSA (L.) Desf. var. AMPLEXICAULIS (Nutt.) S. Wats. in King, Geol. Expl. 40th Par. **5**:345. 1871

Differs from the species in the acute or very short-acuminate leaves which are usually more or less clasping by the sessile base, or by a broadly-winged, short petiole, and are usually broadest toward the base.

The variety ranges from British Columbia and Alberta south through Colorado to Western Texas and California. It appears to be found exclusive of the species in Utah and Nevada and probably also in Idaho and Colorado. Only one specimen from Colorado which seems to be the typical form of the species has been cited. Therefore the origin of the variety was probably in the Great Basin and surrounding mountains. Like the species, it is wanting in treeless regions, and in the Great Basin is rarely found under 6,000 ft. elevation. (Fig. 1.)

This form in American literature has generally been regarded as a distinct species. Dr. Sereno Watson in his "Revision of the North American Liliaceae" so accepted it, although he had previously published it as a variety. Index Kewensis does not list it, however.

Professor Harold St. John, (25) p. 96, in 1929, investigating the genus, reduced it to synonymy. His acquaintance with the group, however, was primarily with specimens of the Pacific Northwest, where intergradation is most marked.

Smilacina amplexicaulis Nutt. ex Baker, Journ. Acad. Philad. **7**:58. 1834.

Unifolium amplexicaule Greene, Bull. Torr. Bot. Cllub, **15**:287. 1888. Based on *S. amplexicaulis* Nutt.

Vagnera amplexicaulis Greene, Man. Bot. Bay Region. 316. 1894. Based on *S. amplexicaulis* Nutt.

Smilacina latifolia Nutt. ex Baker, Journ. Linn. Soc. **15**:570. 1875.

Vagnera pallescens Greene, Proc. Acad. Sci. Philad. 1895:551. 1896.
(Not *V. pallescens* of Heller and many herbaria.)

Smilacina racemosa brachystyla Henderson, Bull. Torr. Club. **27**:357. 1900.

Vagnera amplexicaulis brachystyla Heller, Cat. N. A. Plants, Ed. 2, 4. 1900. Based on *S. racemosa brachystyla* Henderson.

Smilacina amplexicaulis Nutt. var. *glabra* Macbr. Contr. Gray Herb. II **41**:18. 1898.

Vagnera amplexicaulis glabra Abrams, Illust. Fl. Pacif. States. I:453. 1923. Based on *S. a.* Nutt. var. *glabra* Macbr.

Smilacina racemosa (L.) Desf. var. *glabra* St. John, Res. Stud. State College of Wash. **1**:97. 1929. Based on *S. a.* Nutt. var. *glabra* Macbr.

Following is the basis for elimination of each of the above synonyms.

Smilacina latifolia Nutt. A photograph of the type specimen which was examined during this study reveals nothing distinctive in this form from "Rumbia Woods, Rocky Mts." The leaves are broadened toward the base and loosely clasping by a broadly winged petiole. The apex of the leaves tends toward the typical form, being abruptly short-acuminate.

Vagnera pallescens Greene. Greene described this species as differing from "*V. amplexicaulis*" in its smaller size, inclining rather than erect habit, glaucous

rather than bright green aspect, and its range at "higher than middle elevations of the California Sierra, from at least Fresno Co. northward."

One specimen labeled in Greene's handwriting as *V. pallescens* has been seen. This seems a typical, though smaller than average, form of the var. *amplexicaulis*. The only distinguishing feature is the rather short panicle-branches, not mentioned by Greene. The habit of the aerial stem varies too much, even among stems from the same rootstock, to have any weight. Neither can degree of glaucousness or pubescence be regarded as significant when the variation through the range of the form is considered.

From the description this form would be taken for MacBride's "var. *glabra*" published later if it were not that he describes *V. pallescens* as "not glabrous" and the leaves as "stiffly hirtellous beneath."

Smilacina racemosa brachystyla Henderson. *Smilacina racemosa* and *S. amplexicaulis* have been classically considered as being distinguished, among other things, by the longer style of the latter although in the original description its style is mentioned as being "very short." Henderson proposed this variety to cover those western forms which have the leaf shape of the var. *amplexicaulis* but short styles.

In a comparative study made of 15 specimens of each form, selected at random, the styles of *S. racemosa* were found to range from .3 to 1 mm. with an average of .53 mm.; the var. *amplexicaulis* to range from .4 to 1.2 mm. with an average of .75 mm. Among the forms of var. *amplexicaulis*, those with styles less than .7 mm. were from Idaho, Arizona, and Colorado; with styles more than .7 mm., from Oregon, Montana, British Columbia, and Utah.

A study made with such a small number of specimens can hardly be regarded as conclusive, especially as such short lengths are difficult to measure accurately; yet the results do indicate that there may be a tendency for styles to average longer in the Western form. The extreme variability of this factor throughout North America, however, makes it impossible to regard it as a basis for another variety.

Smilacina amplexicaulis Nutt. var. *glabra* Macbr. is based on a wholly glabrous form found at high elevations of the Sierra Nevada from B. C. to California. The leaf type is invariably that of the var. *amplexicaulis*. The plants are generally smaller and more glaucous than is usual for the variety.

This might merit rank as a "forma" of the variety. However pubescence is very variable, and forms which are glabrous on the lower part of the stem and lower leaves, or pubescent only in the inflorescence are frequent and widely distributed. Further, the multiplication of names is awkward.

Glabrous specimens of *S. racemosa* are occasionally found in Texas.

SELECTED SPECIMENS

ALBERTA: Rosedale, Wooded Hills, 2200-2500 ft., June 15, 1915, Marion E. Moodie 931, (MBG 800647).

ARIZONA: Monument Peak, Chiricahua Mts., north slope, in aspen woods, 8500 ft., September 27, 1906, J. C. Blumer Pr. 133, (This is labeled "type of *S. Blumeri*

Greene," an unpublished name. This is a small form resembling Rydberg's *V. australis*. Some specimens from this locality have a subspicate inflorescence, the flowers growing in umbelliform clusters along the axis.) (US 563499).

CALIFORNIA: Jonesville, Butte Co., 2100 meters, June 16, 1931, E. B. Copeland 616, (MBG 1021630); Sancelitos Hills, March 31, 1869; A. Kellogg & W. G. W. Hartford 996, (MBG 146942); Cisco, Yuba River, 5500 ft., June 17, 1917, A. A. Heller 12706, (glabrous form), (MBG 825288).

COLORADO: Norwood Hill, San Miguel Co., Moist north slopes, 7000 ft., August 16, 1912, Ernest P. Walker 468, (US 543797); Near Pagosa Peak, S. Colo., August 3, 1899, C. F. Baker 256 (labeled "*S. glomerata* Greene," an unpublished name. The panicle-branches are very short and compact.) (US 543797); Flagstaff Mt., Boulder, June 25, 1906, F. Daniels 143, (MBG 146931).

IDAHO: Hereford R. S., 7500 ft., June 7, 1928, W. P. Cottam, (BY 3023); Oxford, May 6, 1885, F. E. Leonard 43, (NY); Henry's Lake & Mt. Chauvet, 10,000 ft., July 7, 1897, Rydb. & Bessey 3879, (NY); Tamarack, Washington Co., (MBG 146928).

MONTANA: (Missoula, Woods, May, 1917, J. A. Hughes 1061, (MBG 895666).

NEVADA: Mt. City, Mill Creek, in aspens, 7000 ft., August 14, 1912, A. Nelson & J. F. MacBride 2208, (MBG 712043).

NEW MEXICO: Harvey's upper ranch, Pecos R. National Forest, 9600 ft., August 1, 1908, P. C. Standley 4613, (MBG 146967); Gila National Forest, under douglas-fir, 8000 ft., (labeled "*S. glomerata* Greene ined."), (US 583102).

OREGON: Alpine meadows on east side of Crater Lake, July 23, 1935, J. Wm. Thompson 12273, (glabrous form, labeled "topotype of *S. racemosa* var. *glabra* (Macbr.) St. John"), (US 1650522); Harbrook Gulch, 4700 ft., July 15, 1897, E. P. Sheldon 8578, (MBG 146962).

TEXAS: Davis Mts., Jeff Davis Co., moist shaded slope at foot of high, north facing bluff of Mt. Livermore, 2300 meters, June 1, 1928, E. J. Palmer 34293, (NY), (MBG 946427). (Glabrous form).

UTAH: Mouth of Logan Canyon, Cache Co., Zundel 169, (NY); Uintah Mountains, 8000 ft., June 27, 1927, W. P. Cottam (BY 2409); Aspen Grove, North Fork, Provo, Sept. 1, 1934, B. F. Harrison, (BY 6521); Zion Canyon, 4500 ft., April 24, 1930, W. P. Cottam, (BY 4774); Arch Canyon, 7000 ft., June 26, 1927, W. P. Cottam, (BY 2434).

WASHINGTON: Rumbia Woods, Rocky Mts., (Columbia River?), 6/33 (?) Nuttall, (labeled as "type of *S. latifolia* Nutt."), (NY) (photograph only); Mt. Paddo, June 14, 1890, W. N. Suksdorf 1006, (MBG 146969); Lake Chelan, Cascade Mts., 1915, A. S. Kammerer 119, (MBG 789950).

WYOMING: Woods, rolling plains between Sheridan and Buffalo, Wyoming, 6000 ft., Frank Tweedy 2513 (NY); Hoback Canyon, Teton Co., June 24, 1932, 8000 ft., L. Williams & R. Pierson 713, (MBG 1032739).

Smilacina racemosa (L.) Desf. approaching var. *amplexicaulis*, (Nutt.) S. Wats.

ARIZONA: Head of Black River, White Mts., damp places, July 18, 1912, L. N. Goodding 1207, (US 661913).

CALIFORNIA: Lassen's Peak, Calif., August, 1896, R. M. Auston, (labeled "*S. petiolata* Greene," an unpublished name. The leaves are only acute but spreading, on long petioles), (US 294693).

CHIHUAHUA: Sierra Madre, 1899, Barber & Townsend 8, (US 739667); Las Cuevas, June 30, 1892, C. V. Hartman 544, (US 306037).

2. SMILACINA STELLATA (L.) Desf. Ann. Mus. Paris 9:52. 1807.

Rootstock long, white, 2-4 mm. in diameter; aerial stems numerous, erect, spreading or arcuate, straight or flexuous, 20-70 cm. long, 2-5 or rarely as much as 7 mm. in diameter, puberulent; leaves 5-15 or rarely 20 cm. long, flat or folded, often distichous, green or pale and glaucous, puberulent, linear-lanceolate to lanceolate or falcate, more or less clasping at the base, obtuse to acuminate at apex; inflorescence a simple raceme, sessile or short-peduncled, 1-20 flowered, the rachis often zig-zag; pedicels 2-15 mm. long, erect to spreading; perianth-segments 3-6 mm. long, 1-1.5 mm. wide, white or greenish; stamens slightly shorter than the perianth-segments; fruit a globose berry about 8-9 mm. in diameter, at first light green with 6 blue longitudinal stripes, later turning dark blue or sometimes red throughout.

Found throughout the United States except in those states lying south of Virginia and Kansas and east of New Mexico; also in Southern Canada from Newfoundland, Prince Edward Island, and New Brunswick to British Columbia; in Alaska, and Chihuahua. (Fig. 2.) Specimens from Norway and Sweden, presumably escaped from cultivation, have also been seen.

This species tends to grow in denser colonies and to frequent more open areas than *S. racemosa*. However the two are sometimes found near each other, especially in the western United States.

Perhaps because of its wide distribution, this species is very variable in such characters as habit of the plant and size and shape of the various parts. Many of these forms have been given specific or varietal rank. However the complete intergradation and lack of any definite geographical limitation make it impossible to retain these, with one exception.

Convallaria stellata L. Sp. Pl. 316. 1753.

Tovaria stellata Neck. Elem. **3**:190. 1790. (name only). Based on *C. stellata* L.

Maianthemum stellatum Link, Enum. pl. Hort. Berol. **1**:343. 1821. Based on *C. stellata* L.

Unifolium stellatum Greene, Bull. Torr. Bot. Club **15**:287. 1888. Based on *C. stellata* L.

Vagnera stellata Morong, Mem. Torr. Bot. Club. **5**:114. 1894. Based on *C. stellata* L.

Smilacina sessilifolia Nutt., ex Baker, Journ. Linn. Soc. **14**:566. 1875.

Tovaria sessilifolia Baker, l. c., based on *S. sessilifolia* of Nuttall's Mss.

Unifolium sessilifolium Greene Bull. Torr. Bot. Club **15**:287. 1888. Based on *T. sessilifolia* Baker.

Vagnera sessilifolia Greene, Man. Bot. Bay Region 316. 1894. Based on *T. sessilifolia* Baker.

Smilacina stellata sessilifolia Henderson, Bull. Torr. Club **27**:358. 1900. Based on *T. sessilifolia* Baker.

Unifolium liliaceum Greene, Pittonia **1**:280. 1889.

Vagnera liliacea Rydb. Mem. N. Y. Bot. Gard. **1**:101. 1900. Based on *U. liliaceum* Greene.

Vagnera leptopetala Rydb. Bull. Torr. Bot. Club **28**:268. 1902.

Vagnera valida Greene, ex Baker, West. Amer. Pl. **1**:19. 1902. (Name only).

Vagnera pallescens of most herbaria and Heller's collection No. 8641 of June 28, 1907, from the "Truckee Pass east of Reno, Nevada." Not *V. pallescens* Greene.

The basis for elimination of each synonym follows.

Tovaria sessilifolia Baker. This name has been much misunderstood and variously applied, largely because of the great variation and intergradation among western forms of *S. stellata*. As originally given by Baker, the description includes all western forms with flexuous stem and rachis and pedicels more than 3 lines (about 7 mm.) long. This includes a multitude of forms, and is not in itself exclusive. Specimens are often found east of the Mississippi with flexuous stems or rachis and rarely with pedicels as much as 9 mm. long, while in the West, flexuous stems with short pedicels, or long pedicels with straight stem and rachis are common.

In the East, *S. stellata* usually grows in dense colonies in rather open places. There the aerial stems are erect and usually rather short and stout, glaucous, and the leaves are ascending, rather narrow and often folded, and scattered around the stem. The pedicels are short and stout, and the rachis straight.

In the western area it grows in both open and shaded places. In its most extreme form, the shade-loving plant has, as would be expected, a weak, slender, flexuous, spreading stem; broad, flat, thin, distichous leaves which are scarcely at all glaucous; and an open, few-flowered inflorescence with long, slender pedicels and zig-zag rachis. The rootstocks are more slender, and the individual plants tend to be more scattered.

This most extreme shade form is common in the Northwest Coastal region, from British Columbia to Southern Alberta, Wyoming, and Northern California. (This is the same area in which intergradation is most evident between *S. racemosa* and the var. *amplexicaulis*.)

Every conceivable intergrade between this shade-loving plant and the plant of more open places is found, in these states and many others. From the Southern Rocky Mountains and Southern California are found plants which retain the long pedicels, but tend to be more robust, with stout, though often arcuate, straighter stems, straight rachis, and longer leaves. Arizona and New Mexico specimens are found which are scarcely distinguishable from the Northwest coast form except for the narrower, long-acuminate leaves. Specimens are found in every Western state which are not distinguishable from the Eastern form, along with every possible intergrade.

Index Kewensis gives this species recognition.

Unifolium liliaceum Greene. This name was applied to a rather robust form found in the mountains of southern California (and elsewhere) with erect, straight stem; scattered, bright green, "falcate" leaves, and long, ascending pedicels. Similar specimens are common which have varying degrees of glaucousness; these, except for rather longer pedicels, are not distinguishable from robust specimens of the more typical eastern form. Other specimens are common which differ from Greene's description only in having an arcuate stem and lanceolate, rather than falcate, leaves.

Vagnera leptopetala Rydb. was based on a form found most commonly in the mountains of Wyoming, Colorado, and New Mexico. It is characterized

by small size of all the parts, with narrow perianth segments; short, weak, arcuate stem; and narrow, flat, distichous leaves. Rydberg describes it as being "pale," but forms otherwise similar but of a bright green color are common in the same area. Except for the arcuate stem and distichous leaves, it is not distinguishable from small specimens of more typical *S. stellata*, and intergrading material is abundant.

Vagnera valida Greene. Specimens bearing this name are occasionally found in herbaria; one has been seen which was also labeled as the type of "*Smilacina Greenei* Gates ined." This name seems to have never been published. The specimens seen have all been robust, bright green forms with distichous, acuminate leaves. Some have the lower flowers in the raceme abortive. Most of them were collected at "King's Canyon, Ormsby Co., Nevada."

Vagnera pallescens of most herbaria and Heller's collection. This is an extremely vigorous form. A typical specimen has a straight, erect stem 70 cm. high and 7 mm. in thickness with scattered, slightly folded leaves to 21 cm. long, glaucous green and acuminate. The flowers are large and numerous, on long (to 13 mm.) stout, spreading pedicels, from a straight rachis. Many of the specimens show pairing of one or more pedicels, as in *S. dahurica* of Eastern Asia.

These plants are among the largest seen, and except for many intergrading forms, might rank as a variety. This was probably the plant Heller had in mind when he listed *V. pallescens* in his *Catalog of Plants of North America*. He may have confused the name with one of Greene's many unpublished "species," most likely *Vagnera valida*.

SELECTED SPECIMENS

ALASKA: Upper Matanuska Valley, Common in drier woods, August, 1913, Ralph W. Chaney 92, (MBG 741699).

ALBERTA: Wood Buffalo Park, Mackenzie Basin, east shore of Lake Mamawi, 58° 35′ N., 111° 22′ W., granite hill, August 8, 1930, Hugh M. Raup 2016, (US 1678408).

CALIFORNIA: Coldwater Canyon, San Antonio Mts., San Bernardino Co., July 12, 1902, Leroy Abrams 2708, (very large), (NY); McAdams (?) Greek, Siskiyou Co., wet meadow, May 15, 1910, Geo. D. Butler 1343, (labeled "*V. lileacea* Greene, from original station," stems 80 cm. long, leaves to 3 × 13 cm., long-acuminate, pedicels to 11 cm. long, rather slender, plant glaucous, (US 669312).

CHIHUAHUA: Near Colonia Garcia in the Sierra Madres, 7500 ft., June 16, 1899, C. H. Townsend & C. M. Barber 35, (US 383159).

COLORADO: Near 4th of July Mine, July 29, 1906, Frances Ramaley & W. W. Robbins 2436, (RM 56940); Chick Creek, 9500 ft., June 27, 1898, Baker, Earle & Tracy 147, (NY), Pagosa Peak, August 5, 1899, Baker 257, (NY); Dark Canyon, Pike's Peak, 9700 ft., July 22, 1901, Clements 242, (NY); Headwaters of Sangre de Cristo Creek, 9000 ft., June 22, 1900, Rydberg & Vreeland 6441, (type of *V. leptopetala* Rydb.), (NY).

DISTRICT OF COLUMBIA: Margin of Island, Washington, D. C., May 12, 1918, E. L. Wherry, (this has bright green leaves and erect, curved pedicels up to 7 mm. long), (US 983792); "Difficult Run of River," Washington, D. C., May 7, 1874 (in flower) and July 5, 1879 (fruiting), Lester F. Ward, (US 134742); along Potomac above Washington, D. C., May 11, 1916, Paul G. Russell, pedicels to 9 mm. long).

IDAHO: Shoshone, May 27, 1899, D. Alton Saunders 3235, (a large form, labeled *S. Greenei*), (MBG 146973).

MICHIGAN: St. Joseph, May 23, 1913, J. A. Nieuwland 11070, (this has pedicels in pairs, one in 3's on lower part of raceme), (MBG 711708).

MINNESOTA: U. S. Govt. Prop. Sec. 20, Minnesota Point, Duluth, in large colonies, under shrubs, in gravel and sand, August 31, 1936, Olga Lakela 1803, ("Large"), (FM 901512); Olga Lakela 1802, ("Small"), (FM 901528), "The large form grows in distinct colonies from the smaller."

NEVADA: King's Canyon, Ormsby Co., 1700-2000 meters, June 10, 1902, C. F. Baker 1038, (labeled "Type of *S. Greenei* n. sp. Gates, Aug. 1915" on MBG specimen, also "*Vagnera valida* Greene n. sp., det. by Greene," tall, stout, leaves large, lanceolate, dark green and glaucous, lower flowers abortive, one born below upper leaf, upper flowers well developed on rather short pedicels, rachis straight), (MBG 146972), (US) (RM43941); Same as above but smaller, with normal inflorescence (RM 157613); Truckee Pass, E. of Reno, June 28, 1907, Heller 8641, (labeled "*V. pallescens* Greene"), (NY, also in most other large herbaria); "N. W. Nevada," July, 1867, W. W. Bailey 1169, (US 36053).

SWEDEN: Upsala, 1869, R. Olberg, (one specimen has forked inflorescence), (US 60100).

UTAH: Provo River, 4550 ft., May 28, 1933, B. F. Harrison (BY 6166); Clear Creek, 5500 ft., June 7, 1928, W. P. Cottam, (BY 2999); Head of Moon Lake, Ashley Forest, 8100 ft., June 7, 1928, B. F. Harrison, (BY 7644).

WYOMING: Lonetree, 7200 ft., June 20, 1934, B. F. Harrison & E. Larsen, (BY 7914).

2a. SMILACINA STELLATA (L.) Desf. var. CRASSA Victorin, Contrib. Lab. Bot. Univ. Montreal 14:16. 1922

Differs from the typical eastern form in the fleshy, relatively broad leaves; the thick but short stem; and the maritime habitat. The leaves are usually numerous and crowded, the stem reddish, and the whole plant extremely glaucous when young, glabrescent in age, when the veins appear unusually prominent. The type specimen has ovate, rounded leaves; others examined are narrower and acute.

This variety seems to be confined to the region of the Gulf of St. Lawrence, and is largely an island form, though it is occasionally found in the interior of Quebec. Victorin states that it is found in marshy areas and is the halophytic form of the species (30, pp. 16-17.) (Fig. 2.)

Further study and collections are needed of this interesting but little-known form. It seems to be quite distinct both morphologically and ecologically, though a few specimens have been seen which appear to be intermediate.

SPECIMENS EXAMINED

NEW BRUNSWICK: Grand Menace, J. L. Rothrock, (FM).

QUEBEC: Archipel de Mingan, Ile Nue, sur un îlôt, bird sanctuary, July 9, 1926, Victorin & Rolland 24249, (type), (MV, UM); Alright Island, Magdalen Islands, sand ridge bordering the strand at the narrows, August 21, 1912, Fernald, Long & St. John 7194 (MV); Natashquan, sur les dunes de l'embouchure, July 28, 1929, Victorin & Germain 28191, (MV, US 1522312); Natashquan, sur les dunes du côte sud d l'estuaire, July 21, 1924, Victorin & Rolland 18480, (UM); Archipel de Mingan: Ile a Bouleau, sur les rivages, August 4, 1924, Victorin & Rolland 18532, (UM); Iles de

la Madelaine, Ile Brion, sur les dunes, communes, August 3, 1919, Victorin & Rolland 9849, (UM); Carleton, Ca. de Bonaventure, La Gaspesie, sur les graviers secs du barachois, August 12, 1930, Victorin & Rolland 33561, (UM); Iles de la Madelaine, Havre aux Maisons, July 24, 1919, Victorin & Rolland, (UM).

3. SMILACINA TRIFOLIA (L.) Desf. Ann. Mus. Paris 9:52. 1807

Rootstocks very long and slender, scaly; aerial stems low, 5-30 cm. long, glabrous, the sterile shoots with usually 2 leaves and the fertile ones 3-5. Leaves lanceolate or oblanceolate to elliptic, acuminate, acute, or rounded at apex and tapering to a sheathing base, 3-13 cm. long, 1-4 cm. broad; inflorescence a simple raceme, 2-12 flowered, pedunculate; pedicels spreading or ascending, 2-10 mm. long; berry 5-6 mm. in diameter, dark red, turning blue in drying.

This species has a rather spotty distribution in the colder temperate regions of North America and Siberia. It is found in a broad belt from Connecticut to Minnesota, Newfoundland, Labrador, and Manitoba; appears occasionally in the Mackenzie Basin, Alberta, and Montana; and in Siberia is found in the vicinity of the Zea River. It is found only in cold, acid soil in Sphagnum bogs. (Fig. 2.)

Convallaria trifolia L. Sp. Pl. 316. 1753.
Unifolium trifolium Greene, Bull. Torr. Bot. Club, **15**:287. 1888. Based on *C. trifolia* L.
Vagnera trifolia Morong, Mem. Torr. Bot. Club, **5**:114. 1894. Based on *C. trifolia* L.
Smilacina trifoliata Desf., according to Barclay, New Cycl. Amer. Hort. 1672. 1906.
Vagnera pumila Standl. Smithsonian Misc. Coll. 56, No. 33:1. 1912.

Vagnera pumila was described from a collection of depauperate material in Alberta. It was described as distinguishable by the dwarf size, short leaves much exceeded by the inflorescence, less spreading pedicels, and short, thick style. These characters can all be matched in depauperate specimens collected in the eastern portion of the range (New York, Wisconsin, etc.). The style on the Standley collection is shorter than usual for the species; however this character may vary considerably, even on individual flowers on the same plant. Other specimens seen from Alberta are like the typical forms.

SELECTED SPECIMENS

ALBERTA: Slave Lake District, Damp Forest, N. Atauwau River (Salteau), June 6, 1929, A. H. Brinkham 4165, (NY); Prairie Creek, Western Alberta, July 3, 1911, J. H. Riley 100, (type of *V. pumila* Standl.), US 622636); Wood Buffalo Park, Mackenzie Basin, Moose (Eight) Lake District, about 59° 36′ N, 113° 7′ W., Muskeg E. of ranger station, August 12, 1929, Hugh M. Raup 2019, (NY).

MANITOBA: 1898, E. S. Thompson, (MBG 1147243).

MICHIGAN: Reese's herb in Thuja bog in openings, June-August, 1917, F. C. & M. T. Gates 10491, (MBG 829791).

MONTANA: G. C. Swallow. (MBG 147076). (This has two leaves, one is 5 cm. broad, amplexicaul, exceeding raceme, petioles 1-2.5 mm. long, plant young).

NEWFOUNDLAND: Vicinity of Balena, Hermitage Bay, Bog, July 7, 1903, Wm. Palmer 1405, (labeled *V. pumila*), (US 492241); Dark Harbor, bogs, May 7, 1896, A. C. Waghorne 40, (MBG 147241).

NEW YORK: "Fiddlers' Green," Peckspt, in deep sphagnum of the "green," June 9,

1916, Wm. R. Maxon 6918, (labeled *V. pumila*), (US 789487).

PRINCE EDWARD ISLAND: July 30, 1901, J. R. Churchill, (MBG 739868).

SIBERIA: Zejskaja Pristań, am Zeaflusse, auf nassen Bergwiesen, June, 1899, I. Dörfler 271, (labeled *V. pumila*), (US 1310274).

VERMONT: Mt. Mansfield, July 2, 1897, J. M. Greenman 1255, (MBG 722196).

WISCONSIN: Brown Co., June 2, 1886, J. H. Scheutte, (labeled *V. pumila*), (US 752322).

Excluded Species

Smilacina alpina, Royle, Illustr. Bot. Himal. 380 = *Clintonia*.
Smilacina bifolia Schult. f. Syst. vii. 307 = *Maianthemum*.
Smilacina borealis Ker-Gawl. in Bot. Mag. 55. 1155, 1403 = *Clintonia*.
Smilacina canadensis Pursh, Fl. Am. Sept. i. 233 = *Maianthemum*.
Smilacina cordifolia Becker, Fl. Frankf. i. 136 = *Maianthemum*.
Smilacina dilatata Nutt. ex Baker, Journ. Linn. Soc. xiv. 563. 1875. = *Maianthemum*.
Smilacina Eschscholtziana Andrz. & Bess. ex Baker, Journ. Linn. Soc. xiv. 564. 1875. = *Maianthemum*.
Smilacina streptopoides Ledeb. Fl. Ross. iv. 128 = *Streptopus*.
Smilacina umbellata Desf. Ann. Mus. Par. 9:53. 1807. = *Clintonia*.
Smilacina uniflora Menz. ex Hook. Fl. Bor. Am. 2:175. t. 190. = *Clintonia*.

Summary

This paper is a taxonomic study of *Smilacina* of Desfontaines growing naturally in temperate North America. The following species and varieties are retained:

Smilacina racemosa (L.) Desf.
Smilacina racemosa (L.) Desf. var. *amplexicaulis* (Nutt.) S. Wats.
Smilacina stellata (L.) Desf.
Smilacina stellata (L.) Desf. var. *crassa* Victorin.
Smilacina trifolia (L.) Desf.

The species retained in the present work are natural and readily distinguishable, the same as those proposed by Linnaeus, later retained by Sereno Watson in his study of the *Liliaceae*, and with one exception, that of *S. sessilifolia*, which is united with *S. stellata* in this study, accepted by Index Kewensis. The varieties have fairly definite geographic limitations and the majority of specimens can be immediately placed, although intermediate forms occur.

ACKNOWLEDGMENTS

Appreciation is here expressed to all individuals and institutions who have contributed in any way to the preparation of this paper. I wish especially to thank Professor B. F. Harrison of Brigham Young University at Provo, Utah for his unfailing encouragement and cooperation, and for his criticism of the manuscript.

I am also indebted to the Missouri Botanical Garden and the New York Botanical Garden for transcripts of unavailable literature, and to the following persons and institutions for the loan of herbarium material:

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BRIGHAM YOUNG UNIVERSITY,
PROVO, UTAH.

Noteworthy Plants of Texas I.

Three New Species from Texas[1]

B. C. Tharp

In the course of field work on the seed plants of Texas over the past quarter century some 80,000 sheets have been added to the mounted material in the University of Texas Herbarium. A goodly number of these have failed to fit any specific descriptions either in manuals or, so far as we have been able to find, in taxonomic literature.

For some years the author has been engaged in assembling material for a proposed manual of the flowering plants of Texas. At the present time the resulting manuscript is being checked against the herbarium. This work brings out the apparent necessity of describing as new species such collections as appear definitely specifically distinct from any species already described, and of publishing supplementary notes or even amended descriptions on some known species. These descriptions will appear from time to time as specimens representing undescribed species are encountered in the checking work.

The following descriptions constitute a beginning of this series.

Thamnosma Aldrichii[2] Tharp, n. sp.

Planta suffruticosa, 3 dm. alta; ramis gracilibus, ascendentibus, fastigiatis, glabris, viridibus, glandularibus; foliis linearibus, 8± mm. longis, plus minusve glandulari-punctatis, sessilibus, viridibus, marginibus minute sinuatis; floribus 2 vel 3 extra-axillaribus apicem ramulorum, pedicellis gracillimus, 2.5 mm. longis; calyce ca. 1.5 mm. lato; petalis 4, usque ad 2 mm. longis, ovatis, obtusis; capsula 3 mm. longa.

Low, subfruticose, much branched at base from a thickened woody taproot, with upright little-branched stems about 30 cm. high, densely fastigiate, glandular; leaf blades linear, about 8 mm. long, more or less glandular punctate, subentire, sessile, at length deciduous; flowers in terminal interrupted racemes, pedicels about 2.5 mm. long; calyx about 1.5 mm. broad, sepals half-orbicular, obtuse; petals purplish-white, ovate, obtuse, glandular punctate, 2 mm. long; stamens 8, shorter than the petals, inner whorl conspicuously shorter than the outer, filaments subulate, glandular punctate, anthers orbicular; capsules glandular punctate, 3 mm. high, 2-lobed, the valves extending to the middle.

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[1] Contribution from the Herbarium, Department of Botany & Bacteriology of the University of Texas.

[2] See pages 550-551: Webb, Walter Prescott. The Texas Rangers; a Century of Frontier Defense. 584 pp. Houghton Mifflin Company, Boston. 1935, and University of Texas Herbarium Biographical Sketches I, page 688 of this volume.

Of the four described American species of *Thamnosma,* this species is most closely related to *T. texana* (A. Gray) Torr. The habit is most strikingly different being densely fastigiate in contrast to the spreading and often subdecumbent and usually open growth of the plants of *T. texana.* This

Fig. 1. Type sheet of *Thamnosma Aldrichii* Tharp. *B. C. Tharp* 43990, Pecos County, Texas, June 6, 1943, in the University of Texas Herbarium.

species is dark green in color as contrasted to the usual yellowish glaucous appearance of *T. texana*. The flowers and fruit of this are also much smaller and the pedicels longer and more slender, the number of flowers in the raceme are fewer. There is also more contrast in length of stamen between the outer and inner series.

This plant seems to be restricted to the desert scrub of west Texas. It occurs from Valverde County to Crane and Brewster Counties, while *T. texana* is distributed from Travis, Goliad, and Cameron Counties west to the area of *T. Aldrichii*, through northern Mexico, north to El Paso County, Texas, and southern Colorado.

Specimens examined (all in the University of Texas Herbarium): TEXAS: BREWSTER COUNTY: Chisos Mountains, 7-18-1932, *C. H. Mueller s.n.;* 10-9-1936, *B. C. Tharp s.n.;* infrequent on low hills above Hot Springs, Chisos Mountain area, 6-8-1937, *Barton H. Warnock 949;* CRANE COUNTY: 6 miles south of Crane, 7-11-1941, *B. C. Tharp s.n.;* PECOS COUNTY: Stockton to Sheffield, 6-3-1940, *B. C. Tharp 43993*, June 6, 1943, *B. C. Tharp 43990* [3] (TYPE), June 9, 1943, mesa margins and slopes, June 25, 1943, low mesa point, June 21, 1943, *43994*, mesa top, July 12, 1943, mesa margin, July 15, 1943, & mesa slopes July 23, 1943; IRION COUNTY: Mertzon, April 1932, *B. C. Tharp s.n.;* Del Rio to Comstock, 4-1-1933, *Eula Whitehouse s.n.*

Anemone edwardsiana Tharp, n. sp.

Herbacea perennis, erecta; cormis brunneis, oblongo-obovatis, 2-4 cm. longis, 1-2 cm. crassis; foliis plurimis, trifoliatis, glabris, petiolis 8-15 cm. longis; petiolulis usque ad 2.5 cm. longis; foliolis reniformibus, usque ad 3.5 latis, profunde 2-4-fidis, lobis crasse crenatis; scapis 2-5 dm. altis, basi glabris, apice pubescentibus; bracteis primariis involucri 3, 2-5 cm. longis; ramulis axillaribus usque ad 3, uterque 2-bracteato sceundario involucro; floribus ad centro circa 2.5-3 cm. latis, aliis parvioribus, periantho viridi-albo; capitulis in fructu oblongo-ellipticis, 1.5-3 cm. longis, 6-8 mm. crassis; achaeniis late, ovatis, marginatis, rostro brevi, erecto, pilis ad basem pubescentem longitudine aequantibus.

Corms brown, oblong-obovate, 2-4 cm. long, 1-2 cm. thick; leaves several, 3-foliolate, glabrous, the petioles 8-15 cm. long; petiolules up to 2.5 cm. long; leaflets reniform in outline, up to 2.5 cm. broad, deeply 2-4 cleft, the lobes coarsely crenate; scapes 2-5 cm .broad, deeply cleft, the lobes coarsely crenate; scapes 2-5 dm. tall, glabrous below, upwardly increasingly pubescent, densely pubescent beneath flowers; primary involucral bracts 3, each 2-5 cm. long, 3-

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[3] Specimens of *Tharp 43990* are being distributed to the Chicago Natural History Museum Herbarium, United States National Herbarium, Arnold Arboretum Herbarium of Harvard University, Missouri Botanical Garden Herbarium, University of California Herbarium at Berkeley, University of Arizona Herbarium, University of Michigan Herbarium, Philadelphia Academy of Natural Science Herbarium, California Academy of Sciences Herbarium, Herbarium of the Catholic University of America, Herbarium of the University of Notre Dame, New York Botanical Garden Herbarium, Gray Herbarium of Harvard University, Herbarium of the Biological Institute of Mexico, and the Herbarium of the Royal Botanical Gardens, Kew, England.

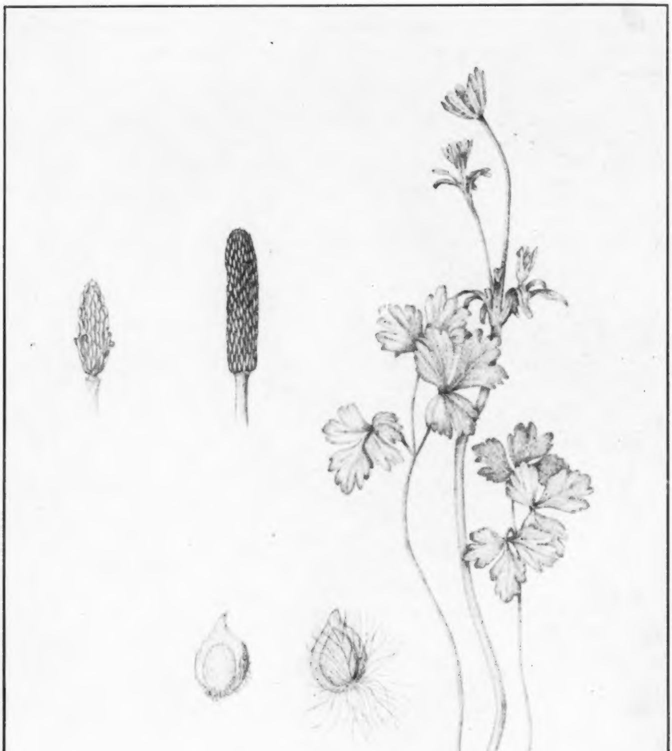

Fig. 2. *Anemone edwardsiana* Tharp, (del. N. Marie Anderson.) (Upper left) Comparison of androecium of *A. edwardsiana* (left) and *A. decapetala*. (Lower left) Comparison of young and mature achene of *A. edwardsiana* (above) and of *A. decapetala* (below).

cleft into linear-oblong divisions (the lateral divisions occasionally 2-cleft) sparingly soft pubescent; lateral branches potentially 3 (one in each bract axil), each with 2 bracts similar to those of the primary involucre except smaller and more densely pubescent, each having a potential bractless flower stalk in its axil; maximum potential number of flowers on each compound scape 10 (1 on the central scape and 3 each on the 3 lateral branches); central flowers ca. 2.5-3 cm. broad, the others smaller, perianth greenish white; fruiting head oblong-elliptic, 1.5-3 cm. long, 6-8 mm. thick; achenes broadly ovate, plump, margined, each with a short erect beak and a tuft of fine basal hairs as long as the pubescent body.

Rich, moist soil along limestone ledges and in shaded locations at the bases of bluffs, Edwards Plateau, (from whence its name,) February to May.

Differs from *A. decapetala* Ard., apparently its nearest relative; in having a branched scape; in smaller flowers which are invariably greenish white (never pink or blue); in its shorter and less dense fruiting spikes; in the less dense pubescence of the achenes, and in the erect beak (the beak of *A. decapetala* being almost horizontal).

Specimens examined (all in the University of Texas Herbarium): TEXAS: BEXAR COUNTY: Creek at Krempkan Divide, 4-11-1926, *E. R. Bogusch 590;* TRAVIS COUNTY: Bull Creek near Austin, 2-22-1926, *E. R. Bogusch 388;* Barton Creek region, 3-10-1916, *B. C. Tharp s.n.;* Austin, 3-16-1922, *B. C. Tharp 1382;* Austin, 3-1-1937, *B. C. Tharp* 4; near dam, 2-22-1908, *H. H. York s.n.* (TYPE).

Hypoxis humilis Tharp, n. sp.

Herbacea perennis acaulescens; cormis circa 1.5 cm. longis, falcatis, fibrosis; foliis lineari-filiformibus, 1-4 dm. longis, circa 2 mm. latis, sparse hirsutis, saepe involutis, marginibus albis; scapis solitariis, filiformibus, teretibus, ut videtur 1-floris; bracteis filiformibus, 4-6 mm. longis, dense pubescentibus; perianthiis primo circa 5 mm. longis demum circa 8 mm. longis, pubescentibus, ovatis, acutis, persistentibus; capsulis globose-pyriformibus, circa 4 mm. longis, circa 3 mm. latis, circumscissilibus; seminibus subglobosis, nigris, minute rugosis, circa 1.2 mm. diametro.

Acaulescent herb from elongated corms, corms about 1.5 cm. long, slightly more than half as thick, curved, frequently simulating root-stocks, scantily covered with fibers; leaf-blades linear-filiform, 1-4 dm. long, about 2 mm. wide sepals about 5 mm. long, slightly hooded, pubescent; petals ovate, acute, green without and yellow within, persistent, about 8 mm. long at maturity of fruit; (but folded so as to appear about 1 mm. wide), sparsely hirsute throughout,

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4 Specimens of *Tharp 43999* are being distributed to the Chicago Natural History Museum Herbarium, United States National Herbarium, Arnold Arboretum Herbarium of Harvard University, Missouri Botanical Garden Herbarium, University of California Herbarium at Berkeley, University of Arizona Herbarium, University of Michigan Herbarium, Philadelphia Academy of Natural Science Herbarium, California Academy of Sciences Herbarium, Herbarium of the Catholic University of America, and the Herbarium of the University of Notre Dame.

more or less involute, white margined, midrib obscure, conspicuously sheathed at the base; scapes solitary, filiform, terete, apparently strictly 1-flowered; bract filiform, 4-6 mm. long, densely pubescent, bearing an apical tuft of long hairs; anthers 1-1.5 mm. long; capsules globose-pyriform, about 4 mm. long, about

Fig. 3. Type sheet of *Anemone edwardsiana* Tharp. *H. H. York*, near dam, Travis County, Texas, February 22, 1908, in the University of Texas Herbarium.

3 mm. broad, circumscissile; seeds subglobose, black, minutely granular-papillose, about 1.2 mm. in diameter.

Closely allied to *H. hirsuta* (L.) Coville, but evidently quite distinct.

Specimens examined (all in the University of Texas Herbarium): TEXAS: AUSTIN COUNTY: in deep sandy prairie, 3 miles north of Belleville, May 7, 1939, *B. C. Tharp 43998* [5] (TYPE); ROBERTSON COUNTY: growing in a sparse stand among grass at the edge of a bog near Newbaden, June 17, 1943, *Fred A. Barkley 13017;* on rather dry portion of the bog near Newbaden, Aug. 8, 1943, *Joseph T. Painter, Gray Waldorf & Fred A. Barkley 13398.*

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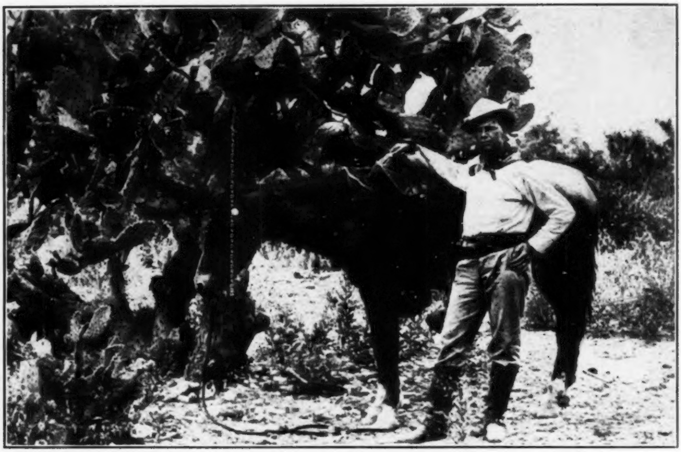
5 Specimens of *Tharp 43998* are being distributed to the Chicago Natural History Museum Herbarium, United States National Herbarium, Arnold Arboretum Herbarium of Harvard University, Missouri Botanical Garden Herbarium, University of California Herbarium at Berkeley, University of Arizona Herbarium, University of Michigan Herbarium, Philadelphia Academy of Natural Science Herbarium, California Academy of Sciences Herbarium, and the Herbarium of the Catholic University of America.

Fig. 4. Type sheet of *Hypoxis humilis* Tharp. *B. C. Tharp* 43998, in deep sandy prairie, 3 miles north of Belleville, Austin County, Texas, May 7, 1939, in the University of Texas Herbarium.

University of Texas Herbarium Biographical Note I.

B. C. Tharp and Fred A. Barkley



Photograph of Roy W. Aldrich taken at Rio Grande City, Texas, in 1915.

ROY W. ALDRICH, Captain of the Texas Rangers, noted authority on the history of Texas, known by and beloved friend of those who admire the natural history of Texas.

Born to Georgia A. Wakeman and Joseph W. Aldrich, September 17, 1869, in Quincy, Illinois. Spent his boyhood in Golden City, Missouri, where his father was a banker. There he apprenticed in banking and gained a love for plants from his mother's garden. Spent most of the year in 1888 in the panhandle of Idaho on a ranch. Ran into and settled in the Cherokee Strip in 1893 where he engaged in banking. Was a second lieutenant in the Spanish-American War in 1898, did mining in the Santa Rita Mountains of Arizona in 1899, spent 1900 in Cape Colony and Natal, Africa. Returned to the banking business in Oklahoma. Moved to Corpus Christi, Texas, in 1907. In 1915 enlisted in the Texas Rangers and was assigned to Rio Grande City. He was moved to headquarters company at Austin in 1916, where he became famous for his exciting exploits on special assignments especially in the border area.

He has made his home in Austin since 1916 on a ranch just east of the city. For many years he maintained a private zoo there. He has built up one of the finest private libraries in the Southwest, especially on Texas and Natural History. He maintains botanical gardens specializing in xerophytes both at Camp Mabry and on his private estate. He also has a notable ethnological collection. He has done much to encourage the naturalist and historian in the Southwest. To anyone interested his grounds, ethnological collection, and library are not only open, but are accompanied by the most gracious hospitality of a Texas gentleman.

Classification of Devonian Nautiloids

Rousseau H. Flower

CONTENTS

Introduction

Prior to 1939, most of the known species of nautiloid cephalopods occurring in the Devonian of North America had never received a more adequate taxonomic treatment than that afforded by the old and too-inclusive form genera used by Hall, Barrande and their contemporaries. In 1939 Kindle and Miller presented a bibliography of American Devonian cephalopods in which an attempt was made to place all of the species in modern genera. While this was highly successful for the Ammonoidea, the results were less fortunate for the Nautiloidea, largely because the published descriptions and figures failed to supply enough information for proper generic determination. The writer has been concerned with the revision of Devonian nautiloids since 1934, and has made various contributions to the solution of the problem. The results of these and other unpublished investigations will eventually be brought together in the form of a monograph. However, the investigation has suffered from many delays and interruptions, and since its completion may be further delayed the present summary of results is presented. This consists of two distinct parts, the first a summary of the genera of Devonian nautiloids, most of which can

be placed in families, and the second a compilation of descriptions of a number of new genera and species which are of more than usual interest.

The present list of genera is not quite complete. In the summer of 1938 the writer was commissioned to undertake a study of the New York Devonian cephalopods by the New York State Museum. The results of this investigation consist of two papers, "Cephalopods of the Tully limestone" and "Middle Devonian cephalopods of New York." These works, submitted to the New York State Museum in 1941, contain the descriptions of a number of genera not included in this work, together with the new species upon which they are based. It should be noted that while the publication of this work will undoubtedly precede the appearance of these studies, it includes much new information, and the present classification is both more modern and more complete, for the proper understanding of the families involves a number of forms which could not be included in studies limited to species from New York.

Complete acknowledgment to all who have aided in this study must await the more comprehensive publication now in preparation. The photographic materials, cameras, and the essential grinding and cutting equipment are those of the University of Cincinnati Museum where this investigation was completed. For some of the specimens described here I am indebted to Dr. J. W. Wells of Ohio State University, Dr. I. G. Reimann of the Buffalo Museum of Science, Dr. R. S. Bassler of the U. S. National Museum, Dr. W. A. Bell of the Canada Geological Survey, Dr. Winifred Goldring of the New York State Museum, and Dr. Wilson Laird of the North Dakota Geological Survey.

Classification of Families and Genera

Many of the generic names now used for the Nautiloidea have never been assigned to families. Indeed, the last comprehensive attempt at a classification which would include all genera in their proper places is that of Hyatt (1900). At the present time this classification cannot be employed for both practical and theoretical reasons. The families are completely inadequate for the reception of the genera now recognized. Further, recent work has shown that Hyatt's major divisions of the Nautiloidea are not natural. The Holochoanites, if recognized on a purely morphological basis, basis do not constitute a large group of which the endoceroids and piloceroids are a part, but instead only a part of the Endoceroidea (Flower, 1941) which includes most of the piloceroids. Holochoanitic structure has been found to be absent in all longiconic pre-Chazyan encoderoids thus far studied in thin section. The Schistochoanites, never very well known, does not appear to be a natural group. The Cyrtochoanites evidently contain a series of isomorphic lines. The Actinoceroidea attained cyrtochoanitic siphuncles independent of all other cephalopods evidently prior to the deposition of the Mauryama beds which appear to be older than the lower Chazy of America. In Chazyan time there appear quite independently cyrtoconic cephalopods with small siphuncles essentially tubular in the early camerae, but expanded in the adult. These are regarded as secondarily cyrtochoanitic cephalopods. Probably the Stereoplasmoceratidae attained cyrtoconic structure independent of the cyrtoconic forms. Expanded segments appear again independently in the Mixochoanites, in the genus *Whitfieldoceras* and probably in the Apsidoceratidae of the Ordovician. The Devonian family Pseudorthoceratidae developed cyrtochoanitic structure independently, and is

traceable to the Middle Silurian orthochoanitic genus *Virgoceras* Flower (1939). The Devonian family Rhadinoceratidae, discussed below, presents another genetic line in which the cyrtochoanitic outline was attained coenogenetically, in a stock probably stemming from the orthochoanitic Bickmoritidae of the Silurian. Quite possible further investigations may reveal still other cases of the appearance of cyrtochoanitic structure in a primitively orthochoanitic stock in the vast array of cyrtochoanitic cyrtoceracones the relationship of which is still uncertain.

While it seems necessary, therefore, to abandon Hyatt's major categories, none of the schemes of classification proposed in recent years (Flowers 1941A, p. 7-9, Schindewolf, 1942), deal to any extent with families or genera. Teichert's Eurysiphonata and Stenosiphonata (1933, also Flower, 1941A), are adopted here, although the groups are used as orders of the subclass Nautiloidea rather than as divisions of the Cephalopoda. Teicher's proposal that these two groups of cephalopods were distinct as far back as the earliest shelled cephalopods does not seem probable at present, but the Eurysiphonata serves to unite the endoceroids (in the broad sense) with the actinoceroids. This relationship has been rejected by Schindewolf (1942) and Kobayashi (1935) but the evidence which they employ is open to quite other interpretations (Flower, 1940, 1941A). Further, the writer (1941A) has traced a connection between the actinoceroids and the endoceroids, in which the ancestry of the actinoceroid is traced back through *Polydesmia* and *Bathmoceras* to *Ellesmeroceras*. While the ellesmeroceroids are now considered as a group apart from the Endoceroidea, from which they differ in lacking endocones, they were formerly included under the term endoceroid, as this name was used by Foerste, Teichert and others.

In the tracing of possible relationships a number of serious problems as yet unsettled, have been encountered. The thick and complex connecting ring appears to be an inherent and a primitive feature of the Eurysiphonata, and one which occurs even in aneuchoanitic endoceroids. Yet this ring appears also in the Tarphyceratidae and also in the genus *Discoceras* of the Ordovicion. In general, Canadian cephalopods appear to possess rings similar to those of *Tarphyceras*, but except for *Discosorus*, Ordovician genera show thin structureless rings, such as characterize the Stenosiphonata. It is still uncertain whether two homeomorphic groups are involved, or whether coiled Ordovician cephalopods are closely related as believed by Hyatt on the basis of gross shell features.

Even with these unsettled problems, Teichert's categories seem superior to any other recent suggestions dealing with the classification of the Nautiloidea. Schindewolf (1942) has more recently presented a very different classification, which it is impossible to employ because the categories are not described. Further, it is necessary to take exception to many of his concepts of relationship and also of the morphology of a number of the crucial genera.

The Eurysiphonata are essentially an early Paleozoic group, and by Devonian time are represented only by the family Sactoceratidae of the Actinoceroidea. The Stenosiphonata contain the greater number of Devonian species. Proper classification of this group is still far from complete, although

progress has been made in recent years from two directions, first by the development of a working hypothesis dealing with the relationships of major categories, and second by the tracing of individual genetic lines in terms of genera and sometimes species, resulting in the recognition of families on a better basis than has previously been possible. As yet the results of these two methods of inquiry into the problem have not been perfectly united into a complete classification but absence of adequate data on the morphology of many genera has proved a serious hindrance which only the discovery of new material can overcome. It is evident, however, that there is sometimes such diversity both in form and internal structure among closely related genera, that no classification can be built upon broad and simple morphological lines which will permit succinct definition, as was attempted in Hyatt's classification as well as in the generalizations of more recent authors. Rather the classification will be more analogous to that adopted for the Brachiopoda, in which the essential features of such groups as the Protremata and Telotremata are not at all evident in many of the genera assigned to these groups.

The pre-Chazyan history of the Stenosiphonata is as yet obscure, and it may be that these divisions cannot be applied to Ozarkian and Canadian genera. However, among the stenosiphonate cephalopods of the Chazyan the following groups were recognized (Flower, 1941) which still seem to be useful divisions in the Ordovician, although descendants of some of these groups vary from the morphological pattern in the Silurian and Devonian:

1. Cephalopods with tubular siphuncles. Orthoconic types of this stock appear to be quite uniform in the Ordovician, but may depart from this definition in the Silurian, as shown by *Harrisoceras* Flower (1939A) and *Virgoceras* Flower (1939) in both of which suborthochoanitic segmas may appear, and in the Devonian the cyrtochoanitic Pseudorthoceratidae developed from this group. Most coiled cephalopods belong in this division, but the relationship of the coiled genera of nautiloids in the Paleozoic admittedly requires much more investigation before it can be interpreted in proper detail.

2. Suborthochoanitic cephalopods. Here the septal necks are essentially orthochoanitic, being parallel to the axis of the shell, but the connecting ring is more or less expanded into the camerae. Occasionally, the septal necks are bent so that it is difficult to class the shell as either orthochoanitic or cyrtochoanitic. The simplest forms of the Chazyan are orthoceracones typified by *Sactorthoceras* Kobayashi. The available information suggests strongly that orthoceracones of this group did not survive the close of the Ordovician. To this stock is traceable the breviconic *Clinoceras* and *Whitfieldoceras*, the Mixochoanites, and also the secondarily cyrtochoanitic cephalopods of the next division. The development of the Mixochoanites has been traced by the writer (Flower, 1941). The phylogeny of this group of cephalopods is more fully discussed in a monograph of the Cincinnatian cephalopods, at present (December, 1944), very close to completion.

3. Secondarily cyrtochoanitic cephalopods. Most cyrtoconic cephalopods of the Chazyan possess small ventral siphuncles which are cyrtochoanitic in the adult but suborthochoanitic in the early stages. In later Orvovician faunas

the suborthochoanitic stage is reduced, and it may be still further reduced and eventually lost in Silurian and younger faunas. Clearly the series is a tachygenetic one. By Chazyan time three families have been differentiated, the Allumettoceratidae (nov.) the Oncoceratidae, and the Valcouroceratidae (nov.). To these is added in the Middle Ordovician the Diestoceratidae. Only the Oncoceratidae have been traced into the Silurian. *Oonoceras* appeared in the Ordovician, survived in the Silurian, and gave rise there to many new generic types. *Rizoceras* and *Cyrtorizoceras*, both of which are reported from both Ordovician and Silurian, are at present only form genera, and the Ordovician and Silurian species represent only a convergence of shell form from isolated branches of the oncoceroid stock.

In Silurian time the oncoceroids underwent a great development producing various form types, some of which developed actinosiphonate structure. Probably many of the Devonian brevicones and cyrtoceracones developed from various of these Silurian genera, but as yet few of the families of Devonian cephalopods have been adequately traced to their Silurian ancestors.

4. A fourth division was erected for the family Stereoplasmoceratidae of Kobayashi, which is confined to the Ordovician. This contains orthoconic shells with nummuloidal siphuncles which become more slender in their growth stages. Its relationships are still uncertain, but probably it represents another development from the suborthochoanitic cephalopods of the second division. This is suggested by recently discovered early stages which approach the suborthochoanitic.

5. Cephalopods which possess broadly cyrtochoanitic segments throughout the phragmocone constitute two unrelated stocks in the Ordovician, the Discosoroidea (Flower, 1940A), and the Actinoceroidea. The Actinoceroidea are here placed in the Eurysiphonata, eliminating them from the stenosiphonate series, leaving in this group only the Discosoroidea. In the investigation of the Cincinnatian cephalopods new representatives of this group have been discovered by which the Ordovician development of the family is clarified, and the relationship of the Ordovician Westonoceratidae and the Silurian Discosoridae are more clearly demonstrated. No Devonian forms have been traced to this stock. The meagre morphological data available for *Alpenoceras* suggest that this genus may be a Discosorid, but are not conclusive. The origin of the Discosoroidea is uncertain; it is not even certain that these forms are properly placed in the Stenosiphonata. On the other hand, there does not seem to be any good reason to include them in the Eurysiphonata. The most closely similar eurysiphonate cephalopods are the Actinoceroidea, but the similarity is marked only in Silurian, not Ordovician members of the Discosoroidea, and even there the differences are great. Teichert (1931) was able to demonstrate the lack of a real relationship between the Discosoridae and the Actinoceroidea long before the Ordovician ancestors of the Discosoridae were recognized. Clearly the resemblance to the actinoceroids is due to a convergent trend in the development of a large nummuloidal siphuncle, and has no genetic significance.

The arrangement of families to which Devonian cephalopod genera are

assigned is designed to fit this scheme of classification as closely as possible. Unfortunately before relationships can be definitely established, much further investigation of Silurian types must be undertaken. The diversified forms present in the American Silurian are known almost completely from dolomitic internal molds. These are not only fragmentary but also almost always unsuitable for the morphological examination by sections which have been applied with considerable success to Ordovician and Devonian forms. Further, the study of relationships of Silurian forms will require an extensive restudy of the cephalopods of the Silurian of Bohemia, preferably with a careful examination of Barrande's original material.

In the following classification those cephalopods traceable to Ordovician forms with tubular siphuncles are placed first. Orthochoanitic orthoceracones are united under the new name Michelinoceratidae. Next are placed the cyrtochoanitic Pseudorthoceratidae, because of their evident derivation from the Michelinoceratidae. This is followed by the coiled families which are essentially orthochoanitic or presumably of orthochoanitic origin. The Rutoceratidae is of uncertain origin in the Silurian, but is placed first among the coiled families because of its dominate gyroconic rather than nautiliconic form. The Centroceratidae and Tetragonoceratidae (nov.) accommodate the remaining coiled orthochoanitic genera. The Rhadinoceratidae follow, being regarded as a cyrtochoanitic family which developed from the orthochoanitic *Bickmorites* of the Silurian. The next family, the Brevicoceratidae, however, traces its ancestry through *Oxygonioceras* and *Oonoceras* to the Ordovician Oncoceratidae. The remaining genera, which are brevicones, cannot at present be placed in any family with certainty. Consequently they are grouped together as genera of uncertain position. In the interest of brevity discussion of many of the unsettled problems relating to the classification of these forms is omitted or reduced, and the evidence upon which this classification is based is presented only briefly.

Kindle and Miller (1939) in their attempt to place the described Devonian nautiloids in modern genera and families, assigned many orthoceracones to *Michelinoceras* and many brevicones to *Acleistoceras*. In many cases further study has shown that these generic determinations must be extensively modified. However, preservation of the essential internal structures is poor in much of the Devonian, both in America and Europe, and adequate information is still lacking for many species, some of which were based upon such poor material that one wonders why they were ever given specific names.

Order EURYSIPHONATA

Suborder (?) ACTINOCEROIDEA Foerste and Teichert

Family SACTOCERATIDAE Troedsson

The Sactoceratidae possess the essential features of the actinoceroids, especially the annulosiphonate deposits, the perispatium, and a radial canal system in the siphuncle. Originally characterized by the small segments in contrast to the Actinoceratidae, and by segments which are not as greatly expanded as those of the Armenoceratidae, they are also distinguished by the

development of simple horizontal radial canals, in contrast to the arc-like canals, sometimes in two series, which develop in some other groups. On this basis the writer placed here *Metarmenoceras*, although its segments are as wide as those in many species of *Armenoceras* (Flower, 1940).

Ormoceras is known to range from the Helderbergian to the Ulsterian in eastern North America. *Metarmenoceras* occurs in the Helderbergian. Kindle and Miller (1939) have listed some species of *Armenoceras* as lower Devonian. These are arctic forms, and it does not seem to the writer that their lower Devonian age is thoroughly established. Nor is it certain whether these forms represent *Armenoceras* or *Metarmenoceras*, since the latter genus was distinguished from *Armenoceras* on the basis of features not shown in the descriptions and illustrations of these species, the compressed central canal and the bilateral symmetry of the radial canal system.

Order STENOSIPHONATA Teichert

Family **Michelinoceratidae** Flower, new name

Teichert and Miller (1936) showed that *Orthoceras* cannot be applied to any cephalopod. They revived the long forgotten genus *Orthoceros*, and designated a type species. The genus is a valid one and as redefined is confined to the Baltic Ordovician. Miller has subsequently employed the family Orthocerotidae as equivalent to the Orthocerotidae of Hyatt (1900). For reasons discussed more fully in the study of the Middle Devonian Cephalopods of New York, now awaiting publication, the family name is rejected as undesirable. *Orthoceras* as a *lapsus calami* should not be perpetuated. Further, it is greatly to be feared that the close similarity between *Orthoceros* and *Orthoceras* will cause more confusion than it will eliminate.

The family Michelinoceratidae is proposed here to include not only those genera formerly assigned to the Orthoceratidae, but also for those orthochoanitic genera previously included in the Cycloceratotidae and Kionoceratidae. It may be best defined as a family erected for orthoconic orthochoanitic cephalopods without regard for the variations in surface ornament. The Cycloceratidae formerly embraced annulated shells with transverse markings. However, *Cycloceras* itself is so little known that no species other than the genotype can be assigned to it, and it is even uncertain whether *Cycloceras* is orthochoanitic. Consequently, no orthochoanitic genus can be placed in the Cycloceratidae with certainty. The Kionoceratidae formerly included orthoconic shells with dominant longitudinal surface markings. *Kionoceras* is a valid genus, but in its present scope consists of two very distinct radicles. Whether the typical (Silurian and Devonian) *Kionoceras* developed from the Ordovician species is exceedingly doubtful, and it is to be suspected that *Kionoceras* itself is a form genus containing morphologically convergent but genetically unrelated types.

Baltoceras Holm, originally placed in the Orthoceratidae by Hyatt, is not included, since it is regarded as a derivative of *Ellesmeroceras* as suggested by Kobayashi (1935) and indicated by Schindewolf (1942). A restudy of the genotype established this relationship on the basis of the structure of the con-

necting rings. It showed further that Schindewolf was incorrect in attributing endocones to the genus.

The genera of Michelinoceratidae recognized in the Devonian are listed below:

Michelinoceras Foerste.—This genus is still far too broad, including the bulk of the species formerly placed in *Orthoceras* which have tubular siphuncles. As at present used, it ranges from Ordovician to Triassic. Restriction of the genus has depended in the past largely upon external features, which are now believed to be rather unreliable. Genera in other families include cyrtochoanitic species formerly placed in *Orthoceras*. *Michelinoceras* will doubtless be restricted much further on the basis of internal deposits of the phragmocone. Such work has not been attempted inasmuch as the writer has felt that it should be preceded by a more extensive study of the many species by sections than has yet been possible.

Geisonoceras Hyatt (1884), (emend. Flower, 1939).—The genus is marked externally by transverse markings in which fine transverse markings are interspersed among stronger and more distant markings suggesting varices of growth. The pattern of the deposits of the phragmocone is very distinctive. Only one typical Devonian species has been recognized, *G. teicherti* Flower of the Onondaga limestone of New York. The genotype is from the Middle Silurian of Bohemia.

Geisonocerina Foerste (1935, p. 22).—In its present state this genus is recognized on the basis of the surface of the shell. It is separated from the externally smooth *Michelinoceras* by the presence of transverse lirae and striae, and from *Geisonoceras* by the absence of periodic thickening of the transverse markings. It is feared that in its present state the genus is not a natural one. Recognized species range from the Ordovician to the Devonian and show considerable diversity in other features.

Kionoceras Hyatt (1884).—Restricted in its present form to shells with longitudinal lirae or ribs, with or without finer markings, which may be both longitudinal and transverse. The genus ranges from the Chazyan to the Tully limestone of the Upper Devonian, but may consist of more than one genetic group. Most Ordovician species are small and slender, with low closely spaced ribs. These present a sharp contrast to the large, often gigantic Silurian species with striae and sometimes also ribs which alternate in strength. The genus is not well developed in the Devonian, but Devonian species are apparently closely allied to their Silurian forerunners.

Protokionoceras Grabau and Shimer (1910).—This genus is set apart from *Kionoceras* on the basis of surface features. Instead of having primary longitudinal lirae or ribs with finer markings, the surface bears a uniform cancellate pattern. Silurian and Devonian.

Striacoceras Flower (1936).—The early growth stages show a surface pattern essentially similar to that of *Protokionoceras*. In the adult the transverse markings become more numerous and the longitudinal markings tend to weaken and finally disappear, so that the ornament of the mature shell is

essentially that of a *Geisonocerina*. The genus is known only from Middle Devonian limestones, appearing in the Middle Devonian (unnamed) of Novaya Zemlya, and in the Schoharie, Onondaga, Cherry Valley and Tully formations of New York.

Arkonoceras Flower, n. gen.—This genus, described in detail below, is a smooth shell, compressed in section, with the siphuncle about half way between the center and the shell wall. It is known at present only from the Middle Devonian genotype, *Orthoceras arkonense* Whiteaves.

Other genera, not recognized in the Devonian, include *Orthoceros*, from the *Orthoceras* limestone of the Scandinavian and Baltic areas, *Anaspyroceras* Shimizu and Obata, emend Flower, *Polygrammoceras* Foerste, *Sactorthoceras* Kobayashi, of the Ordovician *Leurocycloceras* Foerste, *Harrisoceras* Flower, *Virgoceras* Flower, and *Dawsonoceras* Hyatt, of the Silurian.

Family PSEUDORTHOCERATIDAE Flower and Caster

This family has been monographed (Flower, 1939) with discussion of its subfamilies and genera, and the known species have been listed. Subsequent investigations have brought to light a few additional species, but no new genera have been found, and no new information has been found relevant to its morphology or phylogeny. The family is one primarily of orthoceracones descended from the Silurian orthochoanitic *Virgoceras*, in which annulosiphonate deposits have already fused forming a calcareous sheath which must have isolated the cameral tissues from the rest of the organism. In Devonian time the segments of the siphuncle have become cyrtochoanitic. The subfamilies are differentiated on the basis of the form and structure of the deposits of the siphuncle. Genera are recognized on the basis of the form of the shell, the ornament, the aperture, the form of the segments of the siphuncle, and some details in the form of the deposits of the siphuncle and camerae. Primitive members of the family were smooth orthoceracones with simple apertures, but in the family complex ornamentation developed and some cyrtocones and brevicones appeared.

Schindewolf (1942) has figured a line drawing of a specimen which he regards as a *Pseudorthoceras* from the Silurian. This represents a cyrtochoanitic orthoceracone, the siphuncle of which contains a lining. This form is not a *Pseudorthoceras*. The segments of the siphuncle are too short and broad, and the lining is clearly not of segmental origin. The features of this section can be duplicated in many specimens of *Treptoceras* and *Ormoceras*, where the apparent deposit is not an original organic calcareous deposit. Most examples of this common phenomenon show such a "deposit" only on one side of the shell. Such a lining is an inorganic complement of an incomplete internal mold. A few cases are known in which the structure may represent the retention of incomplete siphonal tissues in the shell at the time when matrix invaded the siphuncle, but shells showing this condition are the exception rather than the rule. Such a continuous lining may appear in adoral segments of the siphuncle where no annulosiphonate deposits are present, and may be very

deceptive. However, this same lining has been observed passing over the surface of the annulosiphonate deposits in *Treptoceras,* as well as in vacant camerae lacking the deposits. Insofar as Schindewolf's specimen can be identified from only a line drawing, it appears to be a member of the Sactoceratidae exhibiting such an inorganic deposit; clearly it cannot be a member of the Pseudorthoceratidae.

The Devonian subfamilies and genera of the Pseudorthoceratidae are outlined below only in the briefest form, since they have already been extensivly described.

Subfamily DOLORTHOCERATINAE Flower

Siphonal deposits form a continuous ring at the septal foramen which then grows orad until adjacent deposits fuse. Development of the deposit is only slightly more advanced on the venter than on the dorsum.

Anastomoceras Flower (1939).—Segments of siphuncle with neck scarcely recurved; deposits greatly and irregularly thickened in siphuncle. Known only from the Helderbergian.

Dolorthoceras Miller (1931).—Brim at least one half the neck; area of adnation one half the neck. Oriskanian to Pennsylvanian. Best developed in the Hamilton shales.

Diagoceras Flower (1936).—Segments of adult typical of neanic *Dolorthoceras;* sutures strongly oblique. Cherry Valley and Tully limestones.

Spyroceras Hyatt (1884). Essentially a *Dolorthoceras* which developed strong annuli and fine longitudinal markings. Doubtfully present in the Helderbergian. Ranges from the Schoharie grit to the Ithaca shale in New York; present in Middle Devonian of western North America and in Germany, probably England, and Bohemia. Maximum development in the Hamilton of New York.

Palmeroceras Flower (1936).—Siphuncle intermediate between that of *Dolorthoceras* and *Adnatoceras;* exterior finely cancellate. Cherry Valley limestone; doubtfully present in higher beds of the Hamilton.

Geisonoceroides Flower, n. gen. (1936).—A *Dolorthoceras* with annuli and fine transverse striae; invariably very slender shells. Range: Onondaga limestone, Hamilton of western New York and Ontario. Doubtfully present in the Ithaca shale.

Sceptrites Flower (1939).—Section compressed, apex cyrtoconic. Siphuncle as in *Dolorthoceras.* Onondaga, Columbus and Tully limestones; doubtfully identified in the Devonian of Bohemia.

Fusicoceras Flower (1939).—A breviconic shell depressed in section, with dorsal lobes, and a ventral siphuncle similar to that of *Dolorthoceras* in form and deposits. Known only from the Hamilton of western New York.

Cryptorthoceras Flower (1939).—Distinguished from *Dolorthoceras* by

the broadly depressed section, the aperture which is triangular and opens on the ventral side of the shell. Hamilton of western New York.

Adnatoceras Flower (1939).—A smooth orthoceracone characterized by a siphuncle with brim and area of adnation greater than the neck, and connecting rings usually parallel-sided in the middle of the segment. Ranges from the Hamilton to the Pennsylvanian, but best developed from the Tully to the Senecan.

Petryoceras Flower (1939).—Orthoceracones differing from *Dolorthoceras* in having surface markings of transverse zig-zag bands. Known only from the Sherburne sandstone of New York.

(?) *Cyrtospyroceras* Flower (1938).—Differs from *Spyroceras* in the cyrtoconic apex and the ventral siphuncle. Middle Devonian and Senecan of New York.

(?) *Neocycloceras* Flower and Caster (1935).—Annulated orthoceracones with fine transverse markings. Siphuncle nummuloidal, segments rounded in outline, nearly as broad as long. Conewango group, Upper Devonian, New York and Pennsylvania.

Subfamily CAYUTOCERATINAE Flower

Siphonal deposits are differentiated into discrete annulosiphonate structures and a continuous covering of a different material.

Cayutoceras Flower (1939).—Segments subquadrate in section; primary annulosiphonate deposits massive; hyposeptal deposits appear in camerae. Known only from the Chemung.

Bradfordoceras Flower and Caster (1935).—Segments subcircular in section; annulosiphonate deposit restricted; no hyposeptal deposits. Sutures definitely oblique and sinuous. Conewango group, New York and Pennsylvania.

Subfamily PSEUDORTHOCERATINAE Flower

Siphonal deposits of uniform material, forming on the venter and fusing to make a continuous lining before growing appreciably toward the dorsum.

Pseudorthoceras Girty (1911).—Segments of siphuncle rounded, siphuncle subcentral. Senecan to Artinskian.

Mooreoceras Miller, Dunbar and Condra (1933).—Similar to Pseudorthoceras but with depressed section, sinuous sutures, and a siphuncle always well ventrad of the center. The genus appears in the Chemung and persists into the Pennsylvanian.

Family RUTOCERATIDAE Hyatt (1884)

This family was originally based upon *Rutoceras* by Hyatt (1884), who later (1900) changed the spelling of the genus to *Ryticeras*, and the family to *Ryticeratidae*. As at present revised, the family contains many of the gen-

era of the Ryticeratidae, Halloceratidae and Hercoceratidae of Hyatt's 1900 classification. I have united these families because it seems impossible to determine any clear features by which they can be differentiated. Restudy of the genera has shown that *Zitteloceras* does not belong here, and no Devonian species can be placed in this genus properly. *Zitteleceras* is confined to the Ordovician, is closely related to true *Cyrtorizoceras,* and is properly placed in the Oncoceratidae, among the secondarily crytochoanitic cephalopods. *Strophiceras* Hyatt, not known in America, is not a member of this family, but is placed in the Centroceratidae, and indeed, is little more than a *Centroceras* specialized by development of nodes and spines.

The family Rutoceratidae as here defined contains longiconic curved and coiled shells characterized by the development of wings, frills, and spines which are either hollow and spout-like or solid. The shells are typically cyrtoconic and gyroconic, but two genera have developed slight impressed zones. The siphuncle is always ventral and is generally orthochoanitic and empty. Several genera, including *Rutoceras* itself, are cyrtochoanitic. A few types are known to have actinosiphonate deposits. Adequate data for separating the genera on the basis of internal structure is lacking, but from the failure of the siphuncles to indicate any clear line of separation which can be correlated with any other features, it is suspected that both the cyrtochoanitic and the actinosiphonate structures may represent specializations within this family. Certainly the group is a closely knit one on the basis of the form of the shell and the spines and frills which express the varices of growth. Further it is one which, except for the Silurian *Trochoceras* and the lower Devonian *Ptenoceras*, is characteristic of the Middle Devonian, and more particularly of Middle Devonian limestones, throughout the world. The frills and spines are expressions of resting stages in the development of the shell, and reflect static stages in the aperture. They remain much more closely spaced than the varices of many gastropods, and apparently were never subjected to any serious resorption prior to further development of the shell. The solid spines superficially resemble those developed in some younger coiled cephalopods of other families. Mississippian and Pennsylvanian genera, however, commonly show the spines appearing alternately on the left and right sides, and not developed at the same growth stage simultaneously on both, as is always the case in the Rutoceratidae.

The genera are arranged here on the basis of the characters of the section, ornament and siphuncle. The arrangement in itself serves as a rough key which will aid in the identification of these forms. Several new genera are noted which are described in the second part of this work.

I. Surface with one pair of lateral wings, nodes or spines. Venter not angulate in cross section, and dorsum only slightly more flattened than the venter.

Trochoceras Barrande.—Silurian of Bohemia. A simple form with lateral wing-like processes.

Ptenoceras Hyatt (1884).—This differs from *Trochoceras* mainly in the

presence of deposits in the siphuncle, which appear annular in longitudinal section and may or may not be actinosiphonate as Foerste (1926) suggested. The genus is known from the Lower Devonian of Europe, but occurs only in the Onondaga limestone in America.

Roussanoffoceras Foerste (1925).—Lower Devonian of Novaya Zemlya, Onondaga of New York, and doubtfully in the Middle Devonian of Bohemia. Lateral processes are replaced by annuli, which may be complete ventrally, but are reduced there and are absent dorsally.

Ptyssoceras Foerste (1926).—Middle Devonian of Bohemia and western North America. A cyrtocone with one pair of small spout-like processes.

II. One pair of solid spines; venter angled in section, dorsum flat or concave.

Diademoceras Flower, n. gen.—A gyroceracone with the above features. Type, *D. palmeri* Flower, n. sp. of the Cherry Valley limestone. Other species are from the Winnipegosis and Manitoban dolomites.

Threaroceras Flower, n. gen.—Similar in section to the above, but an involute shell with a prominent impressed zone, where the sutures form saddles.

III. Forms similar to the first division except for the involution of the shell and the development of an impressed zone. *Hercoceras* Barrande is the only genus having these features. It is not known in America. *Hercoceras auriculum* Parks is a *Baeopleuroceras*.

IV. Alate to frilled genera.

Halloceras Hyatt (1884).—Shell gyroconic, with frills at the varices of growth. At their juncture with the shell wall the frills describe not only a hyponomic sinus but a pair of lateral sinuses, which represent the bases of regions in which the frills were produced into wing-like processes. This genus serves to connect the preceding forms with *Goldringia*. It is well developed in the Onondaga limestone of New York.

Goldringia Flower, n. gen.—This genus, described below, is characterized by crenulated frills developed at the varices of growth. Such shells have formerly and incorrectly been included in *Rutoceras;* which has spout-like spines only imperfectly connected by short and incomplete frills, and differs from *Goldringia* in having a cyrtochoanitic siphuncle. Goldringia is well developed in the Onondaga of New York, Ontario, and the Columbus limestone of Ohio. The genotype is the widespread *Gyroceras cyclops* Hall.

Centrolitoceras Flower, n. gen.—This genus, based upon the new species *C. perplexum* of the Winnipegosis dolomite of Manitoba, is a gyroceracone similar to Goldringia in the early stages, but with frills which shows no trace of a hyponomic sinus. Adorally the frills are wanting and the shell shows only rugose lines of growth. The genus is known at present only from the genotype.

V. Shells possessing a ventral face flanked by a pair of rows of spines or nodes, and at least one additional pair of lateral spines.

Rutoceras Hyatt (1884).—Conch gyroconic, with a ventral cyrtochoanitic siphuncle. Actinosiphonate deposits have not been observed, but their absence has not been conclusively demonstrated. In addition to the spout-like spines flanking the ventral face, two lateral series are present in the early stages, of which one may be suppressed in the region of the mature living chamber. The spout-like spines are imperfectly connected by short and generally incomplete frills. The cyrtochoanitic siphuncle, the well defined ventral face, and the presence of spout-like spines which dominate the frills all serve to separate this genus from *Goldringia*. Confusion over the characters of the genus is largely due to Hyatt's description, which seems to have been influenced more by species here included in *Goldringia* than by the genotype. Insofar as the extant descriptions of the genotype indicate, *Kophinoceras* Hyatt is a synonym of *Rutoceras*. Its siphuncle has not been observed. *Rutoceras* occurs in the Schoharie of eastern New York, the basal Onondaga of southern Ontario, possibly of Schoharie age, and occurs in the Middle Devonian of Europe.

Adelphoceras Barrande (See Foerste, 1926, p. 379).—The shell is loosely coiled, the dorsum faintly concave, the sides with two rows of late lateral spines on each side. The siphuncle is ventral. The form of its segments has not been observed, but its interior is known to contain actinosiphonate deposits. Foerste regards the form as slightly trochoceroid. It is dubious, however, whether the concave dorsum indicates the development of an impressed zone. A similar concavity of the dorsum is found in gyroconic species of *Tetranodoceras* and *Hindeoceras*.

Homoadelphoceras Foerste (1926).—This genus was separated from *Adelphoceras* on the basis of the convexity of the dorsum in cross section, and the gyroconic rather than the faintly trochoceroid curvature of the shell. The need for this genus seems questionable since the concavity of the dorsum in *Adelphoceras* does not necessarily represent a true impressed zone, and the trochoceroid condition is slight and even dubious. Neither genus appears in America, but both are confined to the Middle Devonian of Europe.

Tetranodoceras Flower (1936).—Shell with three rows of nodes or spines on each side in addition to the pair flanking the ventral face. The siphuncle differs from that of *Adelphoceras* and also of *Homoadelphoceras* in being orthochoanitic and free from organic deposits. The genus occurs in the Middle Devonian of New York and Illinois.

Hindeoceras Flower, n. gen.—This genus, based upon *Gyroceras canadense* Whiteaves of the Winnipegosis dolomite, is erected for coiled shells with a pair of spines flanking the ventral face, and in addition more than four rows of spines which are lateral and extend at uniform intervals well onto the dorsal side, typically forming a circle of spines at each resting stage of the aperture which surround the entire whorl, although the spines become smaller on the dorsum. The siphuncle is ventral, tubular and empty. The genus is well developed in northern and western North America and in Europe.

Casteroceras Flower (1936).—Shell cyrtoconic, the mature part essentially straight. The hyponomic sinus is reduced, and the spines flanking the ventral

face are not markedly different from the others in position. Ten or eleven rows of spines occur around the circumference of the shell, and unlike *Hindeoceras* the spines are uniform in size on dorsum and venter. The siphuncle is ventral, tubular and empty. This genus occurs in the Cherry Valley limestone of New York, the Winnipegosis and Manitoban dolomites, and again in the Middle Devonian of China.

VI. Shells retaining only the spines flanking the ventral face.

Tylorthoceras Miller.—Shell straight, section depressed. Siphuncle ventral, tubular, empty. Ventral face marked by a pair of longitudinally elongated spines which recur at regular intervals. This genus is believed to be a modification of *Casteroceras*. It occurs in the Columbus limestone of Ohio, and in New York in the Onondaga limestone and the Stafford limestone.

Family CENTROCERATIDAE Hyatt

Shells gyroconic to tarphyceraconic and nautiliconic in coiling, characterized by a quadrangular cross section in which the abdominal and umbilical zones are represented by sharp angles, and are only rarely narrowly rounded, and in which the ventral face is much narrower than the dorsal face, the sides being flattened and converging from dorsum to venter. The growth lines of the surface show the presence of a hyponomic sinus on the ventral face. The lateral face is divided in the center by a crest, best seen in the early stages of *Centroceras*, where it is also elevated on a slight ridge, so that the section is obscurely hexagonal. Growth lines are transverse dorsally. The sutures develop lobes on the venter and on the sides, but are transverse dorsally. The siphuncle is tubular and close to but not in contact with the venter.

Hyatt (1900) included here only the genera *Centroceras* and *Tetragonoceras*. Flower (1936, p. 54) suggested that *Tetragonoceras* was closer to *Diadiploceras* as defined by Hyatt, and that *Homaloceras*, placed by Hyatt in the Ophidioceratidae, was probably more closely allied to the Centroceratidae. At the present time a more complete revision is attempted, and the Centroceratidae, on the basis of the above definition is considered as including the following genera:

Homaloceras Whiteaves (1891).—Shell cyrtoconic to gyroconic. Abdominal angles well developed, ventral face slightly concave. Shell very strongly compressed in section. This genus is known only from the Winnipegosis dolomite of Manitoba, where the genotype, *H. planatum* Whiteaves, occurs with one undescribed species. The genus has not yet been recognized in Europe.

Centroceras Hyatt (1884).—Conch tarphyceraconic, the whorls in contact, but with no impressed zone. Both dorsum and venter are flattened and separated from the sides by sharp angles which tend to become crenulate, developing small nodes, in the genotype. Other species, however, show the angles less clearly developed. The lateral faces bear conspicuous crests, which lie on revolving ridges in early growth stages, but in the mature shell the ridges are obscure, the crests are reduced, and come to lie well dorsad of the center. The genus is represented in the Cherry Valley limestone of New York by the genotype.

Undescribed species represent it in the Pine Point limestone of the Great Slave Lake region, and the Columbus limestone of Ohio. Other species of the American Devonian have been placed in *Centroceras*, but restudy has shown that they belong elsewhere, largely in *Nassauoceras* and *Wellsoceras*.

Strophiceras Hyatt (1884) based upon *Gyroceras binodosum* Sandberger, was placed by Hyatt (1884) in the Rutoceratudae. The location of the sutures and the development of four well defined faces shows that this genus is very closely allied to *Centroceras*, from which it differs mainly in the development of a series of nodes on the lateral face along the line of the lateral crest, as well as a series on the abdominal angles. The genus has not been recognized in America.

Carlloceras Flower and Caster (1935) is essentially an edition of Centroceras with a ventral lobe lost and an impressed zone. This genus was originally placed in the Koninckioceratidae. Further study has shown that the presence of a ventral lobe in the suture is a feature which does not necessarily distinguish this genus from the Centroceratidae.

It is uncertain whether the resemblance of this genus to the Pennsylvanian genus *Domatoceras* represents a real relationship. The two are quite similar in section, but *Domatoceras* possesses a well developed ventral lobe, and is closer in this respect to the adult of *Centroceras*. Early whorls of the Koninckioceratidae are simpler and more rounded in section than in any known Centroceratidae. This fact suggests the possibility that the Pennsylvanian family may have a very different origin, as proposed by Hyatt, who believed that it was represented in the Devonian by the little known genus *Potoceras* Hyatt (1894) which has rounded whorls more like those of the young of *Domatoceras*. Admittedly, the origin of the Carboniferous Koninckioceratidae from either round whorled or quadrate whorled Devonian types requires much further investigation.

Family **Tetragonoceratidae** Flower, n. fam.

Shells coiled, ranging from gyroceracones to shells with a slight impressed zone, quadrangular in section, with the sides diverging from the umbilical to the abdominal angles and widest close to the ventral face. Nodes may develop on the faces and angles. The sutures typically develop lateral lobes, and may possess ventral and dorsal lobes as well. These are best developed in the more compressed forms. The siphuncle is tubular and is typically close to the venter.

This family contrasts strongly with the contemporaneous Centroceratidae in which the sides converge from the umbilical to the abdominal angles. The Tainoceratidae resemble the family superficially but may be distinguished by the nature of the flattened dorsum, which is a modification attendant upon close coiling of the shell, and by the nodes which are not paired but alternate, no two nodes being secreted at the same time on the right and left sides of the shell. Three valid genera constitute this family. The inadequately known *Diadiploceras* is also discussed here briefly. Shells of this family are particularly characteristic of the Middle Devonian of central North America, but are unknown in the Appalachian region.

Tetragonoceras Whiteaves (1891).—Conch gyroceraconic. Section quadrate, the ventral face broader than the dorsal face. Abdominal angles finely crenulate. Sutures with slight lateral and ventral lobes separated by subangular saddles. Siphuncle ventral and tubular. This genus is still known only from *T. gracile,* the genotype, from the Winnipegosis dolomite of the Winnipegosis region. Indeed, the species is known only from Whiteaves' original material, which is unprepossessing but leaves no doubt as to the characters of the genus.

Nassauoceras Miller (1932, p. 42) Genotype, *Nautilus subtuberculatus* Sandberger, Middle Devonian of Germany. This is a coiled shell with the whorls in contact. The venter is broad and flat, the dorsum much narrower. The abdominal angles are modified into a series of nodes. A second series of nodes may develop on the lateral face close to the umbilical angles, and, indeed, both series of nodes may be so modified as to appear to be lateral rather than connnected with the angles separating the faces. The sutures have sight lateral and ventral lobes. Their condition on the dorsum is probably not constant, being sometimes transverse and sometimes developing slight lobes there also. The whorl is typically much higher than wide.

Kindle and Miller (1939) have correctly attributed to this genus *Gyroceras seminodosum* Whitfield of the Columbus limestone of Ohio. Here also the writer places *Gyroceratites ohioensis* Meek and Worthen of the Columbus limestone, *Nautilus* (*Discites*) *ammonis* Hall, *Nautilus inopinatus* Hall of the Dundee limestone of Michigan, and several related forms, as yet undescribed. It has been found desirable to include in this genus species which may lack one or sometimes both series of lateral nodes in the adult, a procedure which is supported by the gradual disappearance of these nodes in several forms, usually as a gerontic phenomenon. The course seems far better than the alternate possibility of the erection of a new genus for such forms as tend to loose the nodes, especially as it is perfectly possible that the genotype, being a shell which shows no gerontic phenomena, might very easily show similar features in its latest growth stages. In its present form, this genus includes species which Hyatt (1884) would have included in *Diadiploceras.*

Diadiploceras Hyatt (1884) is based upon *Nautilus quadratus* Hall according to Hyatt, but this species was never described or illustrated by Hall. Unfortunately this form cannot be recognized, and there is even much uncertainty as to the origin of the specimen which Hyatt had in mind in erecting this genus. The writer found among Hall's material a specimen labeled "*Nautilus quadratus,*" but it does not have the characters of the genus and is, in fact, a fragment of a *Wellsoceras columbiense,* and could not possibly have been the specimen studied by Hyatt. The genotype of *Diadiploceras* cannot be recognized on the basis of the generic description, since Hyatt mentions only features having to do with the phase of preservation by which it can be distinguished from *Nautilus inopinatus.* Thereafter it seems best to admit that the genotype of *Diadiploceras* cannot be recognized, and therefore no other species can be placed in the genus with certainty. Instead of erecting a new genus upon the lines of *Diadiploceras,* it has seemed wiser to extend *Nassauoceras* Miller to include such species as differ from the genotype in the suppression

of one row of nodes, since this feature appears with varying degrees of perfection in a number of species which seem to bridge the gap between *Nassauoceras* and *Diadiploceras* as these genera were originally defined.

Wellsoceras Flower, n. gen.—This genus contains shells of broad whorls in contrast to the compressed whorls of the preceding forms, which tend to become free in the latest growth stages. The sutures develop lateral lobes but are often transverse both ventrally and dorsally. The siphuncle is ventrad of the center and apparently tubular. This genus is described more fully in the second part of this study. The nodes of the early stages show a close relationship between *Wellsoceras* and *Nassauoceras*. Genotype: *Gyroceras columbiense* Whitfield, of the Columbus limestone of Ohio.

Family RHADINOCERATIDAE Hyatt

This family consists largely of stout-whorled rapidly expanding shells with simple sutures, a siphuncle which lies normally dorsad of the center of the shell, is crytochoanitic and empty. The origin of this group of shells has presented a puzzle, but happily the study of the genera has presented a solution.

Examination of *Sphyradoceras* Hyatt shows that its early stages are identical with the adult of *Baeopleuroceras* Williams, in rapid expansion, lateral nodes, a cancellate surface pattern, preservation of the hyponomic sinus in the growth lines, and the gyroconic rather than trochoceroid coiling. Later stages show trochoceroid coiling, the modification of the lateral nodes into costae which cross both the dorsum and venter, and the adult shell is quite unlike *Baeopleuroceras*. The siphuncle remains dorsad of the center, but its structure is unknown. The genus is present in the Schoharie grit, where it is represented by several species including the genotype *S. clio*, and also *S. biton* and *S. discoideum*. It occurs also in the Abitibi River limestone, and in the Middle Devonian of Bohemia.

Baeopleuroceras is known from the Hamilton shales of New York, the Tully limestone of New York and Pennsylvania, and the Middle Devonian of the Kwataboahegan River, where it is represented by *Hercoceras auriculum* Parks. Since this genus is definitely younger than *Sphyradoceras*, it seems probable that the features of *Baeopleuroceras* appear coenogenetically in the early stages of *Sphyradoceras*, and progress by proterogenesis, dominating the shell in *Baeopleuroceras*. If so, it may be that the adult features of *Sphyradoceras* may be of value in indicating the ancestry of the stock. Such features are to be found not in Silurian trochoceroids, which are homeomorphic with *Sphyradoceras* but not related to it, but in the closely allied gyroceraconic genera *Bickmorites* and *Tyrrelloceras*. These are costate shells, round in section, with the hyponomic sinus well developed, and a siphuncle which is central, but orthochoanitic and not cyrtochoanitic. The strong similarities of these forms with *Sphyradoceras* seems to indicate a relationship. Foerste, however, thought that *Sphyradoceras* could be allied with Silurian costate trochoceroids. These forms, typified by *Lechritrochoceras*, are characterized by a dextral spire; that of *Sphyradoceras* is sinistral. The siphuncle is sometimes central, but more often ventral. No impressed zone is ever developed, and

these genera seem to be more distant from *Sphyradoceras* than do *Tyrrelloceras* and *Bickmorites*, genera so closely allied that they may not be distinct.

The remainder of the genera of the Rhadinoceratidae are treated elsewhere by the writer, (Flower, Cephalopods of the Tully limestone, in press), and are presented here in summary form:

Nephriticerina Foerste.—Broad whorled cyrtoconic shells, with longitudinal lirae and finer transverse markings sometimes present. The hyponomic sinus is often reduced or wanting. This genus occurs in the Hamilton of New York and the Alpena limestone of Michigan.

Nephriticeras Hyatt is a coiled shell, which develops an impressed zone. The whorl is broad, and the surface of the shell retains some trace of longitudinal markings at least in the early stages. As delimited by Foerste, the genus seems to grade into *Nephriticerina* on one extreme and *Rhadinoceras* on the other.

Lyrioceras Foerste (1927) is erected for cyrtoconic to slightly involute shells differing from *Nephriticeras* in retaining a pattern of strong revolving lirae throughout life.

Triplooceras Hyatt (1884).—This genus is based upon *Nautilus insperatum* Barrande of the Middle Devonian of Bohemia. The shell is coiled, of about two volutions, and develops a slight impressed zone. The early stages show nodes produced on the internal mold at the intersection of transverse and longitudinal lirae. These disappear adorally. This genus is represented in America by the Hamilton species *Nautilus subliratus* Hall and an undescribed allied form of the Tully limestone.

Rhadinoceras Hyatt (1894).—This genus is now restricted to coiled forms without an impressed zone, the mature living chamber tending to become free, and with only transverse markings on the surface. It is known only from the New York Devonian.

Heracloceras Teichert (1940).—This is a name proposed for *Gigantoceras* Hyatt, which was preoccupied. The type is the Devonian species *Nautilus inelegans*, which is poorly known internally, but appears to be a larger and more compressed derivative of *Rhadinoceras*. The siphuncle is dorsad of the center, but its structure, reported as cyrtochoanitic by Foerste, requires further verification. Silurian species have been assigned to the genus (Foerste, 1924), but differs in their suture pattern from the Devonian type, and may not be congeneric. Such forms are more closely allied, seemingly, to the Silurian genus *Uranoceras*, while typical *Heracloceras* is very closely allied to *Rhadinoceras*.

Endogomphus Flower (1938).—This is a nearly straight shell with longitudinal lirae and a slightly contracted aperture. It appears to be a straight and faintly breviconic modification of *Nephriticerina*. The siphuncle lies between the venter and the concave side of the shell, but the form of the segments has not been observed.

The metropolis of the Rhadinoceratidae appears to be the Hamilton formation of New York, which has yielded most of the known species. Most of the coiled shells are not too perfectly preserved there, and in the present state of our knowledge, it is sometimes exceedingly difficult to determine the disposition of certain species among the coiled genera *Nephriticerina, Triplooceras, Lyrioceras, Nephriticeras, Rhadinoceras* and *Gigantoceras*. Indeed, these genera appear so closely related that the boundaries between them are necessarily rather arbitrary. The difficulty is largely due to the long neglect which has been the lot of *Triplooceras*, not formerly regarded as a member of this family, but placed by Hyatt (1884) in the Rutoceratidae, and subsequently neglected.

Family BREVICOCERATIDAE Flower (1941)

An account of this family, presented before the Paleontological Society, has previously been published only in abstract form. A more complete discussion is contained in the Middle Devonian Nautiloids of New York, now awaiting publication. The shell form is varied, and no single definition can be devised which is at the same time succinct and adequate to embrace all of the genera at present included here. Typical forms are trochoceroids, gyroceracones and brevicones characterized by a flattened dorsum on which the sutures describe broad lobes, a rounded or sometimes subtriangular venter. The sutures may be simple externally, but frequently develop lateral lobes separated by a ventral saddle, and umbilical saddles separate them from the dorsal lobe. The siphuncle is typically ventral, cyrtochoanitic and contains discrete actinosiphonate deposits. The hyponomic sinus persists through most of the family, and there is a tendency for the living chamber to become inflated and then contracted at the aperture. Atypical genera which depart from these features are included, however, on the basis of such close gradation with typical forms that the generic boundaries as recognized are probably arbitrary. Nevertheless, typical members of these genera are so dissimilar that the retention of the distinct generic names seems eminently desirable.

The origin of the family is to be found in the Silurian trochoceroid *Oxygonioceras*, which has a low loose spire and a ventral cyrtochoanitic siphuncle which is empty. This genus is one of the many form deviations which appear to have been derived from *Oonoceras* in Silurian time. Through *Oonoceras*, the stock is traced back to the Oncoceratidae, of the secondarily cyrtochoanitic cephalopods of the Ordovician.

The first genera placed in this family are the Upper Silurian high spired trochoceroids, *Foersteoceras* Ruedemann and *Mitroceras* Hyatt, which differ in section and sutures, but agree in having a flattened dorsum which bears sutural lobes, and a ventral cyrtochoanitic siphuncle in which rudimentary actinosiphonate deposits appear.

The next record of the stock is in the Schoharie grit of the Middle Devonian. Here the flattened dorsum and the dorsal lobes are retained, the typical subtriangular section is developed with the ventral siphuncle containing discrete actinosiphonate deposits. The living chambers are becoming faintly gibbous. The smooth shell bears lines of growth retaining traces of the hyponomic sinus.

Naedyceras is restricted to loosely coiled trochoceroid shells of this pattern which are symmetrical in section and sutures.

The new genus *Gonionaedyceras* based upon *Trochoceras pandion* is erected for species formerly included in *Naedyceras* which are cyrtoconic, but retain as a trace of their trochoceroid ancestry, a cross section which is definitely askew, and in which the sutures are asymmetrical. Prominent angular saddles separate lateral and dorsal lobes on only one side of the shell. These forms occur in the Schoharie and lower Onondaga. An unnamed genus is also to be erected for a series of species developed from this line in which the section remains askew, as do the sutures, but the shell has become essentially straight. Such forms persist into the upper Onondaga limestone.

Another close relative of these if the new genus *Gyronaedyceras*, based upon *Gyroceras validum* Hall, of the Schoharie grit. The shell is gyroconic, and the section is higher than wide. Otherwise it is very similar to *Naedyceras* in both sutures, aperture, and internal structure. This genus persists into the Milwaukee dolomite, where it is represented by *Gyroceras eryx* Hall.

A second gyroconic genus must remain unnamed at present, as it together with its genotype, are described in the forthcoming work already mentioned. This type, important as the link between *Naedyceras* and *Brevicoceras,* is a gyroceracone of broad triangular whorls, retaining cameral and also actinosiphonate deposits. It persists from the Schoharie grit into the Ithaca shales of the Upper Devonian. The younger species become erratic in coiling.

Wissenbachia Foerste is a compressed brevicone, closely allied to *Naedyceras*, but a more rapidly expanding shell and a much shorter one. It appears in America only in the Schoharie grit. The genotype is from the Middle Devonian of Germany.

Brevicoceras Flower, 1938, is typically a large brevicone with the triangular section, sutures with dorsal lobes, and a ventral cyrtochoanitic actinosiphonate siphuncle. It ranges from the Schoharie to the Hamilton.

Small species of *Brevicoceras* appear in the Schoharie, and such forms apparently lose actinosiphonate structure and have narrower siphuncular segments, as do the early stages of typical *Brevicoceras*. Such forms intergrade with *Exocyrtoceras* to such an extent that some species would receive different generic designation if the line were drawn on the basis of the loss of the dorsal lobes, loss of the flattening of the dorsum in cross section, or on the loss of the actinosiphonate deposits, or of the hyponomic sinus of the aperture. The last feature is arbitrarily selected, as it has at least the dubious sanction of long usage and is no worse than any of the others.

Verticoceras Flower (1936) includes species which agree with these small forms of *Brevicoceras* in the form of the living chamber, but are straighter shells in which the dorsum is not more flattened than the venter. These forms occur in Middle Devonian limestones, reappearing finally in the Tully limestone of the Upper Devonian.

Eleusoceras Flower (1938) retains the internal structures of *Brevicoceras*

but loses the hyponomic sinus, the flattening of the dorsum, and the dorsal lobes of the sutures. It is definitely recognized in the Hamilton, but may include some of the little known large brevicones of other parts of the Devonian.

Four other genera are placed here tentatively, because they seem to be more closely related to the small forms of *Brevicoceras, Verticoceras* and *Eleusoceras* than to any other forms, though the writer does not regard this relationship as well demonstrated. These are *Aletoceras* Flower (1937) of the Tully limestone, *Blastocerina* Flower, now known from the Tully limestone as well as from the Conewangoan genotype, which appear to be very close to this stock. With less certainty I include the allied genera *Ovoceras* Flower (1936) and *Anglicornus* Flower and Caster (1935). *Ovoceras* is almost perfectly duplicated by Silurian species of Bohemia which have, however, rather different and larger siphuncles, a resemblance which seems on the basis of the present evidence to be probably isomorphic. Probably *Micronoceras* Flower (1938) is also a member of this same stock, in which the hyponomic sinus is lost, the shell is nearly straight, and the siphuncle is, as in these other genera, small and simple.

Genera of Uncertain Position

A considerable number of the genera of brevicones are as yet of undetermined taxonomic position. It seems wiser to group these together as genera of uncertain affinities, rather than to attempt a classification which will be necessarily synthetic. Some appear to possess actinosiphonate deposits, while others appear to lack them. Teichert has presented a classification of the actinosiphonate genera which he included under the Cyrtoceroidea (1941). His classification is not employed here for several reasons. First, there is reason to believe that actinosiphonate cephalopods do not constitute a genetic group, but instead, that actinosiphonate structure has appeared in several distinct lines of nautiloid development (Flower, 1943). Teichert's classification is convenient and logical, but it is feared that it is not natural. The relationship of the Brevicoceratidae, established on the basis of species which frequently appear to pass from the morphological boundaries of one genus to the next, shows modification of form, of section, of the development and loss of the hyponomic sinus, features which are the criteria of Teichert's families. Further, in this group can be traced not only the appearance of actinosiphonate deposits, but their ultimate loss.

The internal structure and early growth stages are insufficiently known in a number of the genera grouped here. It is hoped that further examination of these features may present clues to their relationship. At the present time, the available information seems to be of such a nature that several possible relationships are suggested all of which cannot be true; yet there is not adequate evidence for the selection of any one hypothesis and the elimination of the others.

The number of genera makes a morphological grouping convenient. It is, however, only approximate.

I. Shells of phragmoceroid aspect.

Bolloceras Foerste (1926), (emend. Flower, 1938). Middle Devonian of Bohemia, and Ithaca shale of New York.

Paraconradoceras Foerste (1926) Middle Devonian of Bohemia; not known in America.

Metaphragmoceras (Flower, 1938) Middle Devonian of Bohemia, Onondaga limestone of New York.

The writer (Flower, 1943) has pointed out the problems involved in the tracing of the relationship of these shells. They may be true phragmoceroids. Internal differences, however, suggest that instead they may represent only a second development of the phragmoceroid form in Devonian time. They differ from Silurian genera in having concave siphunclular segments containing well developed actinosiphonate deposits.

II. Large exogastric brevicones.

Large exogastric brevicones are particularly characteristic of the Devonian, and more particularly of Middle Devonian limestones, in both Europe and America. In Europe these forms are known perhaps best from the Middle Devonian of Bohemia and the more fragmentary remains from Gerolstein in the Eifel area. In America they are well developed in the Alpena, Columbus and Delaware limestones, and are known also from the more sporadic collections of our western Devonian. Unhappily, American shells frequently fail to show the aperture clearly, which has been used extensively, perhaps too extensively, in the recognition of the genera in this group. Also, the internal structure is usually poorly preserved or altogether wanting.

Acleistoceras Hyatt (1884). This genus is still probably too broad (Flower, 1938), and it is uncertain that all species included in it on the basis of form are similar internally. Inadequate knowledge of many of the species, including the genotype, makes proper taxonomic treatment impossible.

Amphicyrtoceras Foerste (1926).—A species of this genus, known typically from the Guelph formation of New York, is reported from the Detroit River series of Michigan. Kindle and Miller (1939, p. 41), suggest that the specific identification may be questionable. The genus is properly Silurian. *Acleistoceras schoharie* Flower (1938) suggests *Amphicyrtoceras* in some features, and suggests that the two genera may be very closely related.

Paracleistoceras Foerste (1926).—An exogastric actinosiphonate genus not as yet recognized in America. Extant data suggests a relationship with *Acleistoceras*.

Cyrtoceras Goldfuss.—A strongly curved genus of the European Devonian. The segments of the siphuncle are faintly concave and actinosiphonate (Foerste, 1926, pl. 35, 36).

Conostichoceras Foerste (1926).—Unknown in America.

Turnoceras Foerste (1926).—This and the above genus are typically large actinosiphonate brevicones with simple apertures lacking a hypoconic sinus, differing in the structure of the siphuncle. A single small species of the Schoharie grit has the features attributed to *Turnoceras* and was placed in that genus by the writer (Flower, 1938).

Poteriocerina Foerste.—Large gibbous exogastric actinosiphonate shells lacking a hyponomic sinus. The genotype is from the Middle Devonian of Bohemia. A considerable number of American species seem to belong here. The extant data suggest a relationship with *Acleistoceras*.

III. Straight to exogastric brevicones.

Cyrtogomphus Flower.—An exogastric genus definitely lacking actinosiphonate structure. Known from the Hamilton of New York and Ontario.

Pachtoceras Foerste.—The genotype is from the Upper Devonian of the Don River. One species from the Conewango group (Flower, 1938) has been placed here.

Karoceras Roussanoff, *Sycoceras* Pictet, and *Mecynoceras* Foerste are unknown in America.

IV. Siphuncle on the concave side of the shell. Conchs generally though sometimes incorrectly, classed as endogastric.

Coelocyrtoceras Foerste, *Eifeloceras* Foerste and *Wadeoceras* Teichert are not known in America.

Danaoceras Foerste.—This typically Silurian genus has been recognized in the Devonian of Australia (Teichert, 1940, 41). An apparently congeneric form occurs in the Alpena limestone.

Alpenoceras Foerste.—The genotype if from the Alpena limestone of Michigan. *Cyrtoceras occidentale* Whiteaves is a typical species. The large broadly expanded ventral siphuncle has a thick organic lining. While somewhat similar linings are known in genera of actinosiphonate affinities, its extreme thickness here suggests that this genus may be a Devonian derivative of the Discosoroidea.

Archiacoceras Foerste.—Unknown in America. The large actinosiphonate siphuncle is dorsal and not ventral, as shown by the position of the septal furrow of the conch (Flower, 1943).

Eudoceras Hyatt 1884, based upon *Trochoceras pandum Hall,* is an inadequately known genus characteristic of the Schoharie. It resembles the Ordovician genus *Rasmussenoceras* Foerste, but its interior is unknown and its relationships uncertain.

Descriptions of Genera and Species

Order EURYSIPHONATA Teichert
Suborder ACTINOCEROIDEA Foerste and Teichert
Family SACTOCERATIDAE Troedsson
ORMOCERAS Stokes

Ormoceras becraftense Flower, n. sp.

Plate 4, Figs. 3-4

Shell orthoconic, large. The type represents a portion of a phragmocone 124 mm. in length, in which the camerae are preserved over the adoral 180 mm., while the adapical portion consists only of the siphuncle. The conch has been flattened by pressure, and is very poorly preserved externally. In its present condition the cross section is flattened, being not over 40 mm. in height where it is 50 mm. in width, the width being parallel to the plane of bedding. The conch expands transversely from 41 mm. to 51 mm. in a length of 60 mm. and attains a width of about 65 mm. at the adoral end of the specimen, with no indication of having attained maturity. The complete shell must have attained a width of 80 mm. and a length of over one and a half feet.

The sutures are straight and transverse. The camerae occur four in a length equal to the adoral shell width of 50 mm. The curvature of the septum is about equal to the depth of the camera. The siphuncle unusually large for *Ormoceras*, lies close to the shell wall adapically, but is more nearly central adorally. Near the adapical end of the preserved part of the phragmocone the siphuncle is 7 mm. in width at the septal foramen, expanding to 15 mm. within the camerae; the segment is 12 mm. in length. The minimum distance from the siphuncle to the shell wall is 7 mm., and the width of the shell is 40 mm. at this point. Farther orad, at an estimated shell width of 58 mm., the siphuncle is 20 mm. from venter to the septal foramen.

Episeptal and hyposeptal deposits occupy the camerae. The annulosiphonate deposits of the siphuncle are typical of the Actinoceroidea, but the adapical segments show the horizontal radial canals typical of the Sactoceratidae. These canals show no bilateral symmetry, but their radial arrangement is not well displayed in cross section.

Discussion.—This *Ormoceras* is distinguished by the relatively deep camerae and unusually large siphuncle, when taken in relation to the diameter of the conch. These features will serve to distinguish it easily from all other congeneric Devonian species known. Indeed, the large size of the siphuncle is faintly suggestive of the Mississippian genus *Rayonnoceras* Croneis. *O. becraftense* differs from typical *Rayonnoceras* in the form of the segments of the siphuncle, the brims being more prolonged in *Rayonnoceras*, and the segments of the siphuncle are more broadly expanded in the camerae. The differences are not, however, very great.

O. becraftense is the first recognizable cephalapod to be recorded from the Becraft limestone. In the large size of the shell and the heavy siphuncle, it

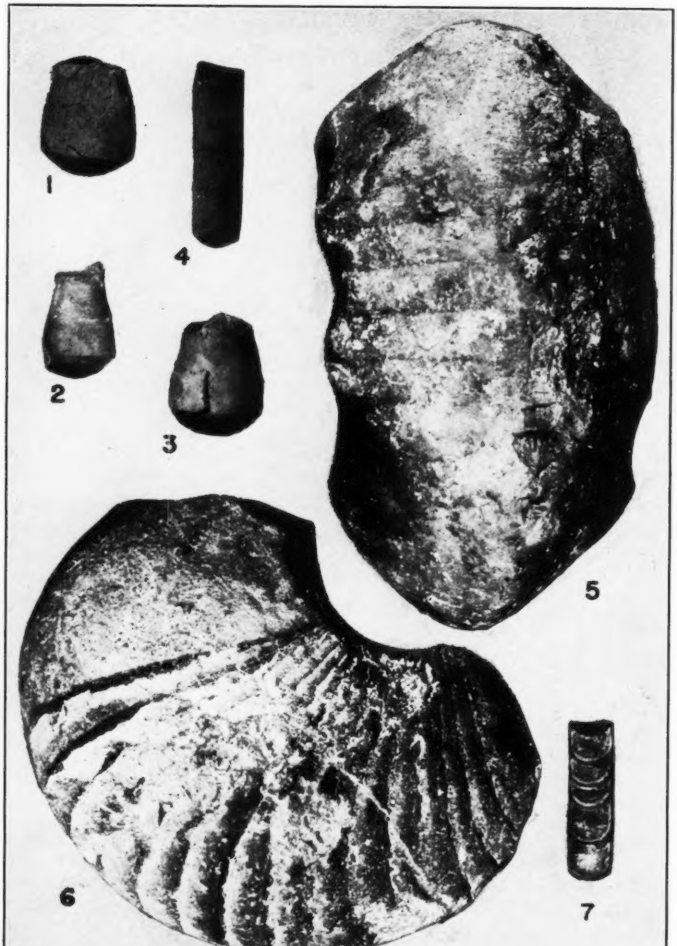


PLATE 1.—Figs. 1-3. *Exocyrtoceras minutum* Flower, n. sp., (1) ventral, (2) lateral and (3) dorsal aspects of holotype, Ohio State University. Eversole chert, Columbus limestone, from Eversole Run, near Columbus, Ohio. Fig. 4, 7. *Arkonoceras arkonense* (Whiteaves). Hypotype, Buffalo Museum of Science, (4) lateral view, (7) vertical section. Olentangy shale, Thedford, Ontario. Fig. 5. *Threaroceras inexpectans* Flower, n. sp. Ventral aspect of holotype, about ×1/2. Ohio State University collection. Columbus limestone, Columbus, Ohio. Fig. 6. *Naedyceras contractum* Flower, n. sp. Holotype, lateral view, about ×1/2. Ohio State University. Delaware limestone, Dublin, Ohio.

presents an unexpected contrast to the actinoceroids already known in the Helderbergian, Oriskanian and Ulsterian. Other species of *Ormoceras* have siphuncles very much smaller in relation to the diameter of the shell. If this species exhibits the remarkable delay in the development of organic deposits of the siphuncle and camerae which is known to occur in other Devonian species of this genus, the extant part of the phragmocone must lie some distance from the living chamber, and the measurements given above, estimating the width and length of the complete shell, are far too conservative.

Only one other cephalopod species has been studied by the writer which is definitely known to come from the Becraft limestone. This is a portion of a small phragmocone showing rounded siphuncular segments, indicating that it also is a representative of *Ormoceras*. This form, however, was too fragmentary to merit description.

Type.—Holotype—collection of the writer.

Occurrence.—From the Becraft limestone, of Kalkberg Ridge, Catskill, New York. Collected at the 1940 meeting of the New York State Geological Association.

Order STENOSIPHONATA Teichert

Family MICHELINOCERATIDAE Flower

Arkonoceras Flower, n. gen.

Genotype: *Orthoceras arkonense* Whiteaves.

This genus is erected for slender orthoceracones of compressed section, the sides being quite strongly flattened though faintly convex, the dorsum and venter narrowly rounded, but also showing faint trace of flattening, so that the section is obscurely subquadrangular. The sutures develop equal rounded dorsal and ventral saddles separated by shallow lateral lobes. The camerae are deep. The center of the siphuncle is located half way between the center of the shell and one wall, presumably the venter. The septal necks are relatively long, sharply bent, and orthochoanitic, extending nearly one fifth the length of the camera. The connecting rings have not been observed. The aperture and ornament of the genotype are unknown.

Discussion.—*Arkonoceras* appears to bear the same form relationship to *Michelinoceras* that *Euloxoceras* bears to the simpler Pseudorthoceratidae. In both, compression of the shell is accompanied by the development of lateral lobes. *Protobactrites* Hyatt is a genus which is at present inadequately known, since the siphuncle of the genotype has not been adequately observed. It is a slender straight shell, but lacks the compressed section and the lateral lobes of *Arkonoceras*. The perplexing *Eobactrites sandbergi* (Barrande) of the Ordovician differs from *Arkonoceras* in its circular section. The septa are modified on the ventral side into a structure regarded as a siphuncle. Further investigation is certainly desirable to determine whether this condition might be analogous instead to the suture pattern of *Bathmoceras*, also shown in a number of the older straight cephalopods, or whether it might be an abnormal phenomenon, such as has been noted in many American Paleozoic cephalopod species and genera.

Bactrites itself differs in the rounded section and marginal siphuncle. *Lobo-*

bactrites is compressed, but also subtriangular in section. Both genera are characterized by marginal siphuncles.

Arkonoceras at present rests only upon the genotype.

Arkonoceras arkonense (Whiteaves)

Plate 1, Figs. 4, 7; Plate 5, Fig. 1

Orthoceras arkonense Whiteaves, 1898, Canada Geol. Surv., Contrib. to Canadian Paleont., vol. 1, pl. 5, p. 406-7, 417, pl. 48, gih. 13, 14, 14a.
———Stauffer, 1908, Ohio Nat., vol. 8, no. 5, p. 276.
———Stauffer, 1909, Ohio Geol. Surv., 4th ser., Bull. 10, p. 149, 182.
———Stauffer, 1915, Canada Geol. Surv., Mem. 34, p. 172.

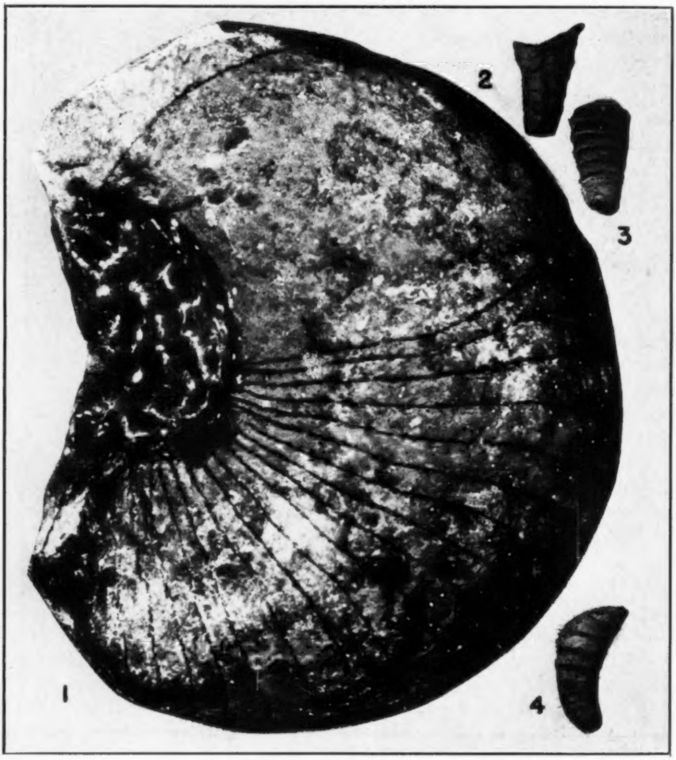


PLATE 2.—Fig. 1. *Naedyceras gibbosum* Flower, n. sp. Holotype, lateral view, ×½. Ohio State University. Columbus limestone, Columbus, Ohio. Figs. 2-4. *Centrolitoceras perplexum* Flower, n. sp. Artificial rubber cast of the holotype, which consists of an external mold. (2) ventral view, (3) dorsal view, (4) lateral view. Geological Survey of Canada collections. Winnipegosis dolomite, Dawson Bay, Lake Winnipegosis, Manitoba. Slightly less than ×1.

Conch orthoceraconic, compressed, antisiphonal side slightly more broadly rounded than siphonal side. The hypotype is 24 mm. in length and expands from 5.5 mm and 7 mm. to 7 mm. and 8 mm. in that length. The sutures describe broad lateral lobes separated by a low saddle on the venter which is arched throughout, and a broader flatter dorsal saddle. The septa are strongly curved, their depth being three-tenths of the shell height. The specimen retains five camerae entire, the last three shorter than the others. The adapical two camerae are slightly greater in depth than the height of the conch, one and one fourth camera occupying a length equal to the shell height. The septal necks are long, being between one fourth and one fifth the depth of the camerae. The connecting rings are not preserved, but must have been tubular. The siphuncle was circular in section, and where the height of the shell is 8 mm. it lies 5.5 mm. from the supposed dorsum, the antisiphonal side, is 1 mm. in diameter, and 2.5 mm. from the venter.

No trace of organic deposits can be seen in either the siphuncle or the camerae. All of the specimen except that part lying orad of the last septum is filled with infiltrated calcite. Possibly the adoral matrix-filled portion represents the base of the living chamber. The length of the living chamber, the surface ornament, if any, and the form of the aperture are unknown.

Discussion.—This species is unique and may be distinguished by the generic characters. No associated orthoceracones are known agreeing even approximately with this form in the small size and very slender shell. However, species of *Bactrites* might be mistaken for this form, but could be distinguished by the marginal siphuncle of *Bactrites*, and by the absence of well defined lateral lobes. The associated *Bactrites arkonensis* is a relatively small shell, expanding more rapidly than *Arkonoceras arkonense*, the section compressed but less flattened and without the faint suggestion of a quadrangular cross section. The camerae are more shallow, and the siphuncle is represented as marginal.

Types.—The two specimens upon which this description is based are, according to the original description in the collections of the Geological Survey of Canada. Unfortunately, they could not be located by the writer there. The hypotype upon which this revision is largely based is from the collections of the Buffalo Museum of Science.

Occurrence.—From the Arkona shale, Middle Devonian, Bartlett's Mills, Ontario, also from the Olentangy shale, Middle Devonian of Thedford, Ontario (Buffalo Museum sp.). The species has also been listed by Stauffer from the Alpena horizon of northern Ohio.

Family PSEUDORTHOCERATIDAE Flower and Caster

Genus SPYROCERAS Hyatt

Spyroceras giganteum Flower, n. sp.

Plate 5, Fig. 3

This species of *Spyroceras* is differentiated from its associates by the very large size and the closely spaced annuli. The holotype is a portion of a straight shell, evidently originally subcircular in section, increasing in width

from 54 mm. to 60 mm. in a length of 60 mm. The sutures are straight and transverse. The septum at the base of the specimen is strongly curved, 14 mm. in depth. There is indication of a subcentral siphuncle. The camerae are very shallow, averaging 7 mm. in depth, so that on this part of the shell approxi-

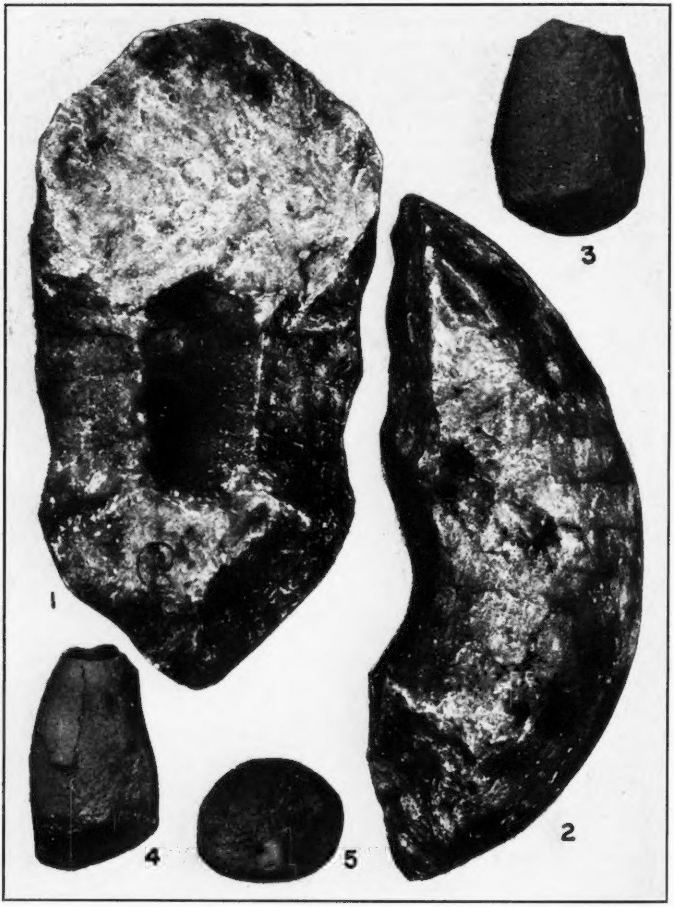


PLATE 3.—Figs. 1-2. *Threaroceras inexpectans* Flower, n. sp., Holotype, ×½, (1) dorsal view, (2) lateral view. Ohio State University no. 193-43. Columbus limestone, Columbus, Ohio. Figs. 3-5. *Exocyrtoceras reimanni* Flower, n. sp. Holotype, Buffalo Museum of Science, (3) ventral, (4) lateral, and (5) apical views. Uppermost Alpena limestone, Centerfield Horizon, Four Mile Dam limestone, from Four Mile Dam, Alpena, Michigan.

mately eight camerae would occupy a length equal to the adoral shell diameter.

The annuli of the shell are low rounded elevations separated by equal concave interspaces. They are so coordinated with the septa that a suture always lies in an interspace between two annuli. The surface markings consist of longitudinal lirae separated by relatively broad interspaces. The lirae are spaced about five in a width of 5 mm. There is very faint suggestion of irregular alternation of weak and strong lirae, but the condition is evidently neither regular nor uniform.

The basal 35 mm. of the phragmocone is occupied by four camerae. It is uncertain whether the adoral portion is really the base of the living chamber or whether the septa there have been destroyed.

Discussion.—This species, by its coarse longitudinal markings and the apparent absence of finer transverse markings, is allied to the associated *S. multicinctum* (Hall) and *S. thoas* (Hall). Although the latter species at least is far too broad, none of the forms included in it appear to approach the present species in size or in the close proximity of the annuli. Both *multicinctum* and *thoas* show indications of geronticism, largely expressed by erratic variations in the spacing of the annuli, at a shell diameter about half that shown by *giganteum*. Indeed, no named *Spyroceras* is as yet known approaching the size shown by this species, and such fragments as are known which remotely approach it in size represent unknown or inadequately described species. *Spyroceras* (?) *rhysum* (Clarke) of the Grand Grève limestone of Gaspé includes among its types a few very large annulated shells. The fine surface markings are unknown, and the annuli are separated by much broader interspaces than in the present species. The Tully limestone contains a species which approaches this one in size, but has the low sharply delimited and distantly spaced annuli which characterize Hamilton and Tully *Spyroceras*. The only other large species are undescribed, and are represented at the present time only by rather inadequate material from the Middle Devonian of Michigan and Nevada.

Holotype.—Collection of the writer.

Occurrence.—From the Schoharie grit, Middle Devonian, Wolf Hill, Albany, Albany County, N. Y.

Family RUTOCERATIDAE Hyatt

Centrolitoceras Flower, n. gen.

Genotype: *Centrolitoceras perplexum* Flower, n. sp.

Conch gyroceraconic, consisting probably of two volutions when complete. Cross section slightly depressed, but with the venter and dorsum equally rounded. The sutures are straight and transverse, the siphuncle tubular and located adjacent to the venter. The surface in the early stages is marked by transverse frills or annuli which show no trace of a hyponomic sinus. At about the termination of the first volution, the annuli have weakened and disappeared, leaving the surface with only coarse lines of growth.

Discussion.—By the frilled exterior and the ventral orthochoanitic siphun-

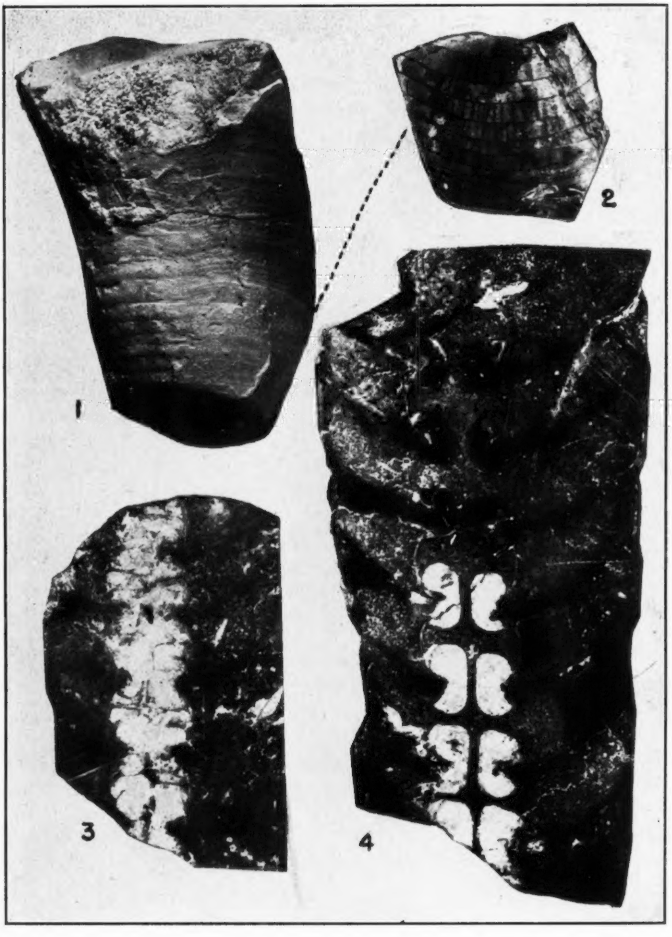


PLATE 4.—Figs. 1-2. *Hipparionoceras iowaense* Flower, n. sp. Holotype, U. S. National Museum, (1) ventral view, showing hyponomic sinus, with profile of left side restored. (2) vertical section from the adapical part of the same specimen. Both ×1. Basal Coralville limestone, Upper Devonian, Volga Valley RR. hill, NE¼ Sec. 13, Center, Iowa. Figs. 3-4. *Ormoceras becraftense* Flower, n. sp. Holotype. (3) vertical section of adapical portion, (4) horizontal section of adoral portion. Becraft limestone, Kalkberg ridge, Catskill, New York. Collection of the writer.

cle, this genus appears to be more closely allied to the Rutoceratidae than to any other group of cephalopods, but is atypical of the family in the equally rounded condition of the dorsum and venter in cross section, as well as in the absence of any trace of a hyponomic sinus.

Superficially *Cyrtospyroceras* Flower (1938) is comparable in possessing annuli and a marginal siphuncle. However, in this genus the annuli are low and rounded, the finer surface markings are longitudinal, the annuli do not disappear adorally, and the shell is cyrtoconic initially instead of gyroconic, and becomes straight adorally. Further, the cyrtochoanitic nature of the ventral siphuncle indicates that there is probably no relationship between this genus and *Centrolitoceras*, but that instead they are contemporaneous convergent types. *Cyrtospyroceras* is probably related to *Spyroceras* of the Pseudorthoceratidae.

Also comparable is the Ordovician genus *Centrocyrtoceras*, which has annuli and a tubular siphuncle. Here the annuli are retained to the mature stage of the shell, and they usually slope apicad forming at least a slight hyponomic sinus. The siphuncle differs from that of *Centrolitoceras* in position, lying slightly ventrad of the center instead of close to the margin.

Centrolitoceras is at present known only from the genotype which is described below.

Centrolitoceras perplexum Flower, n. sp.

Plate 2, Figs. 2-4

The characters of the genus will serve to distinguish this species from all previously described cephalopods. The poor condition of the type does not permit the accurate measurement of the proportions of the shell. The specimen consists of an external mold containing portions of one and one-fourth volutions. The walls were complete ventrally in the earlier portion, but adorally only the dorsum is preserved. At the base the section is circular and 5 mm. in diameter. The width increases to 9 mm. and the height to 7.5 mm. in a ventral length of 10 mm. In this region the segments of the siphuncle are preserved. Between seven and eight segments are found in a length equal to the adoral shell width of 9 mm. The sutures are only faintly indicated, but are straight and transverse. The surface of the shell is marked by sharply elevated annuli which are almost frills as in *Goldringia*. They are separated by broad slightly concave interspaces which show no traces of fine markings. Six occur in the adapical 10 mm. of the shell. In the next quarter volution all traces of the annuli are lost on the dorsum, the only portion preserved, and presumably disappear ventrally also. Instead, fine faintly rugose and rather irregular growth lines appear in this region. The complete shell probably formed whorls not over 60 mm. across.

Discussion.—Although the holotype is represented by an external mold in the Winnepegosis dolomite, a phase of preservation which is most unfavorable for photographic reproduction, it preserves clearly the surface features of the shell, as well as the more crucial of the internal structures. The same, however, is true of the monotypic *Tetragonoceras gracile* Whiteaves, from the same

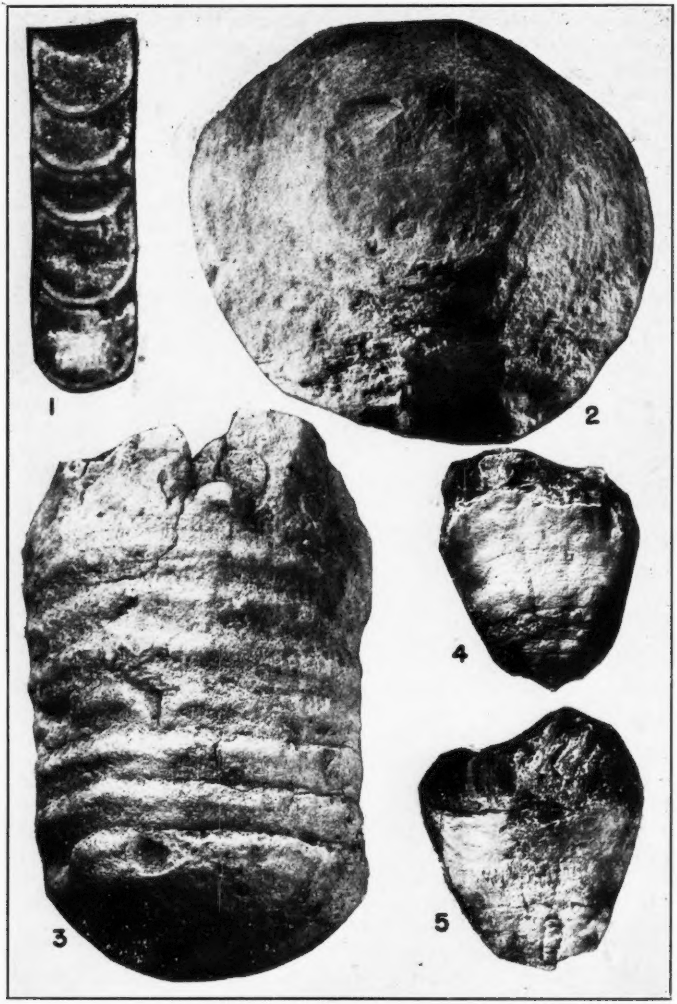


PLATE 5.—Fig. 1. *Arkonoceras arkonense* (Whiteaves) Vertical section of specimen shown in Pl. 1, fig. 4, 7, enlarged about ×2½. Fig. 2. *Hipparionoceras ichnoides* Flower, n. sp. Holotype, septal view. Collection of the writer. Onondaga limestone, Lime Rock, Genesee County, New York. Fig. 3. *Spyroceras giganteum* Flower, n. sp. Holotype, about ×¾, Schoharie grit, Wolf Hill, Albany County, New York. Figs. 4-5. *Hipparionoceras* (?) *lairdi Flower*, n. sp. Holotype, about ×1, (4) dorsal view, (5) ventral view. Watering trough parvafacies, Big Bend Magnafacies, Conewnago group, Upper Devonian. From Summit, Fayette County, Pennsylvania.

formation. Although both forms are poorly preserved from an aesthetic point of view, the remains leave no doubt concerning the specific or generic features in either case. *Centrolitoceras* has not been recognized from any other formation or horizon.

Type.—Holotype, Geological Survey of Canada, Victoria Memorial Museum.

Occurrence.—From the Winnipegosis dolomite, Middle Devonian, Dawson Bay, Lake Winnipegosis, Manitoba.

Goldringia Flower, n. gen.

Genotype: *Gyroceras cyclops* Hall.

Conch gyroceraconic, the whorls describing from one to two volutions, free. Cross section slightly broader than high, the dorsum more flattened than the venter, and the venter typically narrowly rounded so that the section is obscurely subtriangular. The sutures are essentially straight and transverse. The siphuncle is ventral and is tubular, and free from any known organic deposits. The surface of the shell is produced at regular intervals into crenulate frills, each frill bent downward on the venter forming a clear hyponomic sinus. The frills are continuous around the shell, only slightly shorter dorsally than ventrally if at all, and are not complicated by any spout-like or spinous lateral processes. The fine markings consist of transverse lirae and striae which show the crenulate pattern of the frills, and in addition, fainter longitudinal markings are often present.

Discussion.—The species for which this genus is erected have customarily been placed sometimes in *Zitteloceras*, occasionally in *Halloceras* and frequently in *Rutoceras* Hyatt, better known under the emended spelling of *Ryticeras*. However, restudy of the genotypes has made it necessary to restrict these genera. *Rutoceras,* based upon *Cyrtoceras jason* Hall, possess three pairs of spout-like processes on the surface of the shell, one pair flanking the hyponomic sinus, and two other pairs lying farther toward the dorsum. In the late growth stages one of the more lateral pairs may be suppressed. Frills are slightly developed, but are short, and connect the spout-like spinous processes only very imperfectly. Unlike Goldringia, the siphuncle is composed of broadly expanded segments, and the two may, on the basis of this difference in internal structure, not be at all closely related.

Zitteloceras Hyatt has been employed for both Ordovician and Devonian species. However, the Ordovovician genotype shows that the siphuncle is suborthochoanitic to narrowly cyrtochoanitic, the section fails to be subtriangular, and is generally circular, the frills are low and even. The ornament and form suggest very strongly a gradation into the associated genus *Cyrtorizoceras,* and an ultimate origin in the Oncoceratidae, which appears to be the primitive radicle of Ordovician secondarily cyrtochoanitic curved cephalopods.

Goldringia cyclops, the genotype, is a very widely known species. Typically developed in the Onondaga limestone of New York, the species shows considerable variation in proportions, but the examination of a considerable suite of

specimens has failed to show any specific differences between the New York form and that developed in the Columbus limestone of Ohio and the Jeffersonville limestone of Indiana. *Polycronites* Troost (1840) based upon *Polycronites haanii* is possibly based either upon our genotype or a closely allied species. The description is inadequate, the species has never been figured, and insofar as the writer has been able to ascertain the type is not extant. It is impossible to recognize either the genus or the species with certainty.

Cyrtoceras aemulum Hall, *Cyrtoceras ammon* Billings, *Cyrtoceras citum* Hall, *Cyrtoceras eugenium* Hall, *Cyrtoceras trivolve* Conrad and *Gyroceras nereus* Hall are regarded as congeneric. Several additional forms await description. The genus is characteristic of the lower portion of the Middle Devonian, being represented particularly well in the Schoharie grit, the Onondaga limestone, the Jeffersonville limestone of Indiana and the Columbus limestone of Ohio.

Threaroceras Flower, n. gen.

Genotype: *Threaroceras inexpectans* Flower, n. sp.

Conch coiled, the whorls broad and subtriangular, the venter keeled at least in the outer whorl, the sides nearly straight laterad of the keel, but becoming strongly rounded laterally. On the lateral part of the dorsal surface the sides slope slightly dorsad as they approach centrad, but the mid-dorsal area is occupied by a broad shallow rounded impressed zone. The sides of the shell bears a single pair of large nodes on the extreme lateral portion, evidently the internal expression of spines. These are paired as in other *Rutoceratidae*. The sutures are transverse ventrally and laterally, though slightly modified by the nodes. In the impressed zone they develop slight saddles instead of the lobes usually associated with this structure. The genotype fails to preserve the free part of the septa or the siphuncle. Analogy with related forms indicates clearly that the siphuncle is probably ventral and tubular. The surface of the shell bears transverse markings which slope apicad on the venter forming a deep sinus directly in line with the ventral keel.

Discussion.—This unique genus is known at present only from the genotype, which is described below. Its affinities with the Rutoceratidae rather than spinous nautilicones and tarphyceracones of the Carboniferous, which belong to different families, can be detected by the paired condition of the spines and the ventral keel. *Temnocheilus* lacks the ventral keel, and the lateral nodes alternate in arrangement. The affinities of this genus with the Rutoceratidae are largely established, however, by *Diademoceras*, n. gen, described more fully in a work now in press, (Flower, New York State Mus. Bull.), based upon *D. palmeri* from the Cherry Valley limestone of New York. This genus differs from *Threaroceras* in being gyroconic, lacking an impressed zone, possessing slight dorsal lobes, and apparently its surface and section are more uniform in ontogeny, for early stages of a second species from the Manitoban limestone, show that the early whorls retain the section of the adult, while the nature of the impressed zone of *Threaroceras* suggests that the inner whorl lacked at least the ventral keel.

Threaroceras inexpectans Flower, n. sp.
Plate 1, Fig. 5; Plate 3, Fig. 1-2

The unique holotype is a portion of a shell 220 mm. long in actual length, consisting of somewhat less than half a volution of a large coiled shell with a radius of curvature increasing from 110 mm. to 160 mm. and a ventral length of 270 mm. The shell increases from a width of 98 mm. and a height of 60 mm. to a width of 110 mm. and a height of 63 mm. The impressed zone is rounded, concave, and slightly less than one third the width of the shell, being 35 mm. across, and shallow, being 4 mm. deep at the base of the specimen.

The sutures are essentially straight and transverse externally, though irregularly modified by the lateral nodes. The camerae are relatively deep, having a ventral length of 20 mm. where the shell width is 105 mm. The adoral camerae are somewhat shorter showing that the shell approached maturity. Only the basal part of the living chamber is preserved, with a ventral length of 75 mm. Large nodes occur in pairs on the sides of the shell, one row on each side. Three occur in a length equal to the width of the shell. The free part of the septa and the siphuncle are unknown.

The surface markings are very poorly preserved, but show as traces of transverse markings on the holotype. There is indication of a hyponomic sinus on the venter.

Discussion.—This singular form can be distinguished readily by the characters of the genus. The complete shell must have consisted of at least two and probably three volutions, and attained a diameter of at least ten inches. No closely similar species are known, although some gyroconic relatives of this genus await description.

Type.—Holotype, Ohio State University.

Occurrence.—From the Columbus limestone, in the vicinity of Columbus, Ohio.

Hindeoceras Flower, n. gen.

Genotype: *Gyroceras canadense* Whiteaves.

Shell gyroceraconic, large, of about two volutions. Cross section with the dorsum broadly flattened to slightly concave, sides strongly rounded, the venter well arched. Pairs of spines on the surface, reflected by nodes on the internal mold, give the cross section an obscurely faceted appearance. These spines and nodes vary in number. One pair flanks a flattened ventral face. At least four lateral pair are present in addition, and in the typical forms, the rows of spines, spaced about equally around the circumference, cross the dorsum, though the spines decrease in size from venter to dorsum, and dorsally may be so small as to fail to appear as nodes on the internal mold.

The sutures are simple ventrally, and tend to develop broad shallow lobes on the dorsum. The siphuncle lies close to the venter, and is tubular and free from organic deposits.

The surface of the shell bears spines at regular rhythmic intervals, representing varices of growth. In addition, rugose transverse markings are present.

A well developed hynonomic sinus marks the narrow flat ventral face. Otherwise the aperture is essentially transverse, though modified by each of the spines which are typically hollow and spout-like to some extent, although tendencies toward solidification are slightly developed in the genotype.

Discussion.—This genus represents the ultimate development of spinosity in the Rutoceratidae insofar as the typical gyroconic species are concerned.

Its closest relatives are *Tetranodoceras* Flower (1936) in which three pairs of lateral spines are present in addition to the pair flanking the ventral face, but in which the dorsum is free from spines, and *Casteroceras* Flower, a cyrtoconic to orthoconic form with spines continuing around the circumference of the shell, all of equal size, so much so that it is often difficult to determine the ventral face if the siphuncle is not preserved.

Hindeoceras is represented in the Winnigeposis dolomite by the genotype, and also by *Gyroceras filicinctum* (Whiteaves). *Gyroceras logani* Meek of the Devonian of the Mackenzie River is congeneric.

Family TETRAGONOCERATIDAE Flower

Wellsoceras Flower, n. gen.

Genotype: *Gyroceras columbiense* Whitfield.

Shell coiled, the whorls in contact until the mature living chamber is reached, which is free. The cross section is slightly wider than high, and obscurely subquadrangular. The dorsal face is convex and sometimes not clearly defined laterally, though the anbilical shoulders are strongly rounded. The lateral faces are slightly convex and tend to converge very slightly ventrad. The ventral face is slightly arched. All shoulders are rounded. The sutures may be straight and transverse ventrally, or may show a very slight ventral lobe. Well developed lateral lobes occupy the sides of the shell, and are broad and well developed. The sutures describe a broad low saddle on the dorsal face which is flattened slightly but not impressed. The siphuncle lies about half way between the center and the ventral wall of the shell. It has not been observed completely, but has orthochoanitic necks and is presumably tubular. The surface features have not been observed in the genotype, which is free from nodes as far as is known. An allied species, *W. indianense* (Kindle) differs from the genotype mainly in the development of two series of lateral nodes in the inner whorls, causing this part of the shell to resemble *Nassauoceras*. The Columbus limestone, to which the genotype is confined, is a formation unfavorable for the preservation of the early stages of cephalapods, and nodes may be present in the early stage of the genotype also. It is, however, evident that if they are present, they are confined to a shorter and earlier interval of the shell than in *W. indianense*.

Discussion.—This genus is peculiar in its section, coiling, sutures, and the position of the siphuncle. Various of its features suggest possible affinities with the Centroceratidate, the Tetragonoceratidae, and *Heracloceras,* here placed in the Rhadinoceratidae. The evidence of the orthochoanitic septal necks seems to exclude the genus from the Rhadinoceratidae, a conclusion which is confirmed by the nodes of the early stage which suggest an affinity with the

Tetragonoceratidae, and more particularly *Nassauoceras*. The convergence of the sides toward the venter instead of the dorsum suggests the Centroceratidae, but the genus shows no indication of other features of that family. Typical Centroceratidae show the nodes to be developed by modifications of the abdominal and umbilical angles which are typically sharp and well developed. Further, that family is characterized, particularly in the young stages, by the development of lateral crests in the center of the lateral faces, best shown in *Centroceras* itself. The lateral nodes of *Strophiceras* are a modification of these crests.

The presence of two series of lateral nodes in the early stages suggests a relationship with *Nassauoceras*. Although the aperture is obscure, the lateral faces clearly lack the median crests of the Centroceratidae. The siphuncle and sutures further suggest *Nassauoceras*, from which *Wellsoceras* differs in the broader section, the suppression of nodes, the migration of the siphuncle closer to the center of the shell, and such modifications of the sutures as accompany a broadening of the cross section. The relationship between the genera is close enough, to indicate relationship, while differences of a more fundamental nature exist between *Wellsoceras* and members of other families, suggesting that they are homeomorphic to some degree, but unrelated. However, it is by no means certain whether *Wellsoceras* developed from *Nassauocras* by tachygenesis, or whether the nodes appear coenogenetically in *Wellsoceras* and dominate the entire shell in *Nassauoceras*. The two genera are too nearly approximate in age to be interpreted on the basis of the stratigraphic evidence, and the morphological facts are plainly open to more than one interpretation.

The genotype, *W. columbiense* (Whitfield) is one of the commonest species of the Columbus limestone of Ohio. The genus is represented in the equivalent Jeffersonville limestone of Indiana by *W. indianense* (Kindle). Undescribed species represent the genus in the Delaware limestone of Ontario.

Family BREVICOCERATIDAE Flower
NAEDYCERAS Hyatt

Genotype: *Trochoceras eugenium Hall.*

Naedyceras as employed here is revised and somewhat restricted. The shells are loosely coiled, with a very low dextral spire. The section is subtriangular, and is little affected by the asymmetry of the coil. The sutures develop slight lateral lobes, separated by a broad ventral saddle, while umbilical saddles separate them from a broad lobe on the dorsum. The siphuncle is ventral, cyrtochoanitic and actinosiphonate. The section is subtriangular, the dorsum flattened, the venter strongly arched and sometimes obscurely angular. The living chamber tends to be faintly gibbous and the mature aperture is contracted. The surface bears only transverse lines of growth which are often obscure.

As thus defined, *Naedyceras* no longer contains those species which are cyrtoconic rather than trochoceroid, and in which the section and sutures are strongly asymmetric. These forms are set apart in the genus *Gonionaedyceras*.

Naedyceras is represented by a number of described and undescribed species

in the Schoharie grit of New York, and in the Milwaukee dolomite of Wisconsin. These forms are connected stratigraphically and geographically by the two species from the Middle Devonian of Ohio described below.

Naedyceras gibbosum Flower, n. sp.

Plate 2, Fig. 1

This is known from a single specimen which is apparently somewhat flattened laterally by pressure. The shell is 205 mm. long and comprises about one third of a whorl. The dorsal profile is concave throughout, though straighter along the middle of the living chamber than elsewhere. The ventral profile is strongly and nearly uniformly convex. The shell is markedly gibbous. At the base the shell height is 80 mm. This increases to 125 mm. in an eighth of a whorl, then decreases more gradually to 105 mm. at the base of the living chamber, and 95 mm. along the rather oblique aperture. The living chamber has a maximum length of 104 mm., and is 68 mm. long dorsally and 100 mm. long on the venter. The greatest length is lateral, as the result of the lateral lobes of the suture and the inclined aperture. The aperture slopes strongly apicad from dorsum to venter, the entire aperture being modified by the deep hyponomic sinus. The sutures are essentially straight and transverse apically, but adorally lateral lobes develop, the sutures form well defined ventral saddles. The dorsal condition is not clearly shown, but there is indication of the development of slight lobes on the dorsum between umbilical saddles which are low and inconspicuous in this species. The holotype represents a mature shell, from which the apical portion of the phragmocone is missing. If the rate of expansion is as uniform as other species would suggest, this shell probably did not complete quite one volution when entire.

Discussion.—This remarkable species is the largest and most gibbous of the species of *Naedyceras*. In two respects it is somewhat atypical, the combination of rapid expansion of the shell and strong gibbosity, which suggest that unlike other species, this form probably did not complete one entire volution, and the strongly compressed section. There is no certain indication as to how much of the compression of the holotype is natural and how much is due to pressure. The clean condition of the internal mold, the lack of irregularities on the surface and the absence of any indications of such breaks in the shell as frequently accompany flattening, suggest that the section is probably not as greatly compressed by pressure as casual inspection in the light of the broad-whorled Schoharie species would lead one to believe. The type preserves only one side of the shell, but preserves the conch at least from the mid-dorsal to the mid-ventral region. There is only an obscure trace of a trochoceroid condition, and there is no reason to believe that the sutures are asymmetric in their lobation.

The type fails to retain any of the internal structures. It consists of an internal mold which displays the sutures and aperture with great clarity. The present illustration is about one half natural size.

Type.—Holotype, Ohio State University, no. 3685.

Occurrence.—From the Columbus limestone, Middle Devonian, in the vicinity of Columbus, Ohio.

Naedyceras contractum Flower, n. sp.

Plate 1, Fig. 6

This species, known from a single specimen which has possibly been flattened somewhat laterally, resembles *G. gibbosum*, but is considerably smaller, has straighter sutures, a less oblique aperture, and the aperture is more strongly contracted by an adoral increase in the curvature of the ventral part of the shell. The type is 160 mm. long, and has a uniformly concave dorsal profile. The ventral profile is much more strongly curved, the shell increasing gradually in height to a region shortly apicad of the base of the living chamber, and then contracting. In the adoral half of the living chamber the curvature is first greatly increased, and then becomes greatly reduced, the straight part rapidly approaching the dorsum. The conch increases from a basal height of 65 mm. to a maximum height of 105 mm. at the region of the second camera below the living chamber. At the base of the living chamber the height in the plane of the suture is 110 mm., but the suture slopes slightly orad from dorsum to venter, and this measurement is therefore increased by the obliquity. In a length of 30 mm. on the dorsum and 60 mm. on the venter the height decreases to 70 mm. at the apparent aperture.

The sutures form broad low saddles on the venter. On the right side of the shell the sutures are largely convex adorally. On the opposite side they are concave adorally, an indication of lateral flattening which has been slightly oblique. Since flattening has been lateral, this serves as quite conclusive evidence of an original trochoceroid condition not otherwise apparent from the shell in its present condition.

The aperture of the type is probably not quite complete. It is apparently complete ventrally, and possibly also on the dorsal region. If so, the same lateral crests are developed here that are found in some Schoharie species. The septa are preserved as black carbonaceous material. The mural part of the septum can be seen in many instances extending orad from the suture for the greater part of the length of the camera, but not attaining the next adoral suture.

Discussion.—This species is considerably smaller than *N. gibbosum,* from which it differs in the straighter sutures, the less oblique aperture, the more prominent contraction of the living chalber, the more gradual curvature of the shell, and the position of the gibbous region, which is here not far from the base of the living chamber, while in gibbosum it lay well toward the middle of the phragmocone. Unlike gibbosum, this species when complete probably consisted of slightly more than one complete whorl. The present condition of the sutures as a result of flattening indicates the original trochoceroid condition of the shell. The siphuncle is not preserved, nor are the surface markings.

Type.—Holotype, Ohio State University, no. 9553.

Occurrence.—From the Delaware limestone, Middle Devonian, of Dublin, Ohio.

Gonionaedyceras Flower, n. gen.

Genotype: *Trochoceras pandion* Hall.

Shells of this genus are cyrtoconic rather than trochoceroid, most shells failing to complete a single volution. The section is strongly asymmetrical. The dorsum is obliquely flattened, and the section subtriangular, with a strongly rounded to subtriangular ridge of the venter, which is not quite in line with the siphuncle. The sutures bear shallow broad dorsal lobes, umbilical saddles which are sharper on the left than on the right, and indeed may be inconspicuous on the right side, faint lateral lobes, and rounded saddles on the ventral keel. The siphuncle is ventral, cyrtochoanitic, and contains actinosiphonate deposits, believed to be similar to those of *Naedyceras,* although no specimens of this genus have yet been encountered in which they are well enough preserved for detailed study.

This genus is well developed in the Schoharie grit, containing *Trochoceras pandion* Hall, *T. obliquatum* Hall and a number of undescribed species.

Gyronaedyceras Flower, n. gen.

Genotype: *Gyroceras validum* Hall.

Shell gyroceraconic, consisting of about two volutions. The cross section is symmetrical, higher than wide, and more or less triangular. The venter varies from a broadly rounded condition to one in which the sides slope toward a venter so narrowly rounded as to appear subangular. The dorsum, in contrast, is broad and flat. The sutures are relatively simple, being nearly straight and transverse. A slight lobe develops on the dorsum, and faint lobes may develop ventro-laterally separated by a broad obscure ventral saddle. Lobation is never marked. The siphuncle lies close to the ventral wall. The segments are cyrtochoanitic and show the typical discrete actinosiphonate structure of the Brevicoceratidae. The aperture of mature shells may be slightly inflated and then contracted to the aperture, which bears a hyponomic sinus. As in other members of the family, the surface markings consist of transverse lines of growth. Curvature of the mature living chamber may develop here as in *Naedyceras,* but is never as pronounced.

Discussion.—This genus is a compressed cyroceracone, differing from *Naedyceras* in the gyroconic rather than trochoceroid condition of the shell, and in the compressed cross section. In all other features the genera show no constant differences, and their close relationship is evident especially in the light of the internal structure. *Gyronaedyceras* appears in the Schoharie grit, where it is represented by the genotype, and persists to the Milwaukee dolomite of Hamilton age, where it is represented by the large *Gyroceras eryx* and associated species.

Exocyrtoceras Flower 1938

Genotype: *Exocyrtoceras exoticum* Flower.

The shells of this genus are breviconic when slightly coiled, but the more strongly curved species exhibit a slight trochoceroid condition. The section is

strongly depressed, the venter rounded, the dorsum flattened. The sutures typically lack dorsal lobes. The siphuncle is ventral, narrowly cyrtochoanitic, and without known actinosiphonate deposits. The living chamber is gibbous, the aperture contracted, and no hyponomic sinus is developed.

Discussion.—This genus, when first described, was known from the large strongly curved genotype from the upper part of the Columbus limestone, and a group of small cyrtoconic brevicones of the Schoharie grit. The smaller cyrtoconic species are difficult to distinguish from *Brevicoceras*, and the genera are at present separated arbitrarily on the basis of the absence of a hyponomic sinus in *Exocyrtoceras* and its presence in *Brevicoceras*, a character which has the dubious sanction of long usage. It was formerly believed that *Exocyrtoceras* was confined to the lower half of the Middle Devonian. However, the species described below demonstrates its presence in the uppermost Alpena limestone, which Cooper correlates with the Centerfield limestone, at the base of the Ludlowville formation, in New York.

Exocyrtoceras reimanni Flower, n. sp.

Plate 3, Figs. 3-5

The holotype consists of a living chamber. Conch exogastric, depressed, the dorsum more rounded than the venter. The living chamber increases from 20 mm. and 17 mm., the section being depressed, to 22 mm. and 19 mm. in the basal 8 mm., and contracts gradually to the aperture, 17 mm. wide and 12 mm. high, which is attained in a ventral length of 28 mm. and a dorsal length of 24 mm. The aperture is normal to the curving axis of the conch, and the suture at the base of the living chamber is apparently also normal and transverse, the discrepancy between the plane of the aperture and that of the septum being due to the cyrtoconic nature of the shell. The ventral profile is slightly and uniformly convex; the dorsum is convex over the basal two thirds of the living chamber, but becomes concave near the aperture. The lateral profiles are convex, but are most strongly curved in the basal portion. The internal mold lacks the constriction which occurs just before the aperture in so many members of this genus, as well as in the related *Brevicoceras* and *Verticoceras*.

The features of the phragmocone are unknown, except as they are displayed by the septum at the base of the living chamber. The suture is straight and transverse, the siphuncle is small and ventral, being 2 mm. in diameter and 1 mm. from the ventral wall. The septum is rather strongly curved, having a depth of 5 mm., one fourth the width of the shell at this region. The surface of the shell is marked only by faint lines of growth.

Discussion.—In size this species closely approximates *Exocyrtoceras sinuatum* Flower (1928) of the Schoharie grit, but the internal mold of the living chamber is more uniformly contracted toward the aperture, and the greatest diameters occur considerably lower on the living chambers. This species differs from all known members of the genus in the cross section, in which the dorsum is more strongly rounded than the venter. There is in this species no trace of the dorsal lobes developed on the sutures of some of the comparable species.

Type.—Holotype, Buffalo Museum of Science.

Occurrence.—From the uppermost Alpena limestone (Centerfield horizon), now termed the Four Mile Dam formation, from Four Mile Dam, Alpena, Michigan. Collected by Dr. I. G. Reimann.

Exocyrtoceras minutum Flower, n. sp.

Plate 1, Figs. 1-3

Holotype, a small living chamber to which is attached a portion of the phragmocone. The living chamber has a maximum length of 13 mm., and a basal height of 11 mm. and a width of 13.5 mm. The conch is faintly gibbous over the lower two thirds of the living chamber, and then is more or less produced to the aperture, which is 7 mm. high and 10 mm. broad.

The suture at the base of the living chambers develops a shallow inconspicuous lobe on the venter, and a narrower and slightly more prominent one on the dorsum. The cross section shows the dorsum to be slightly more flattened than the venter.

The aperture bears a low rounded crest on the dorsum, very slight lateral sinuses, and appears to rise into a crest on the venter. The extreme mid-ventral region is not clearly enough preserved to determine with certainty whether a very slight hyponomic sinus is present, but there is no reason to assume any such structure. The siphuncle is small and ventral.

Discussion.—This is the smallest of the small brevicones of *Exocyrtoceras* and *Brevicoceras* of the lower Ulsterian. It is much smaller than *Exocyrtoceras micron* Flower (1938) of the Schoharie grit of New York, with which it agrees closely in the suture pattern, and in general form. However, this form is not only smaller than *micron,* but contracts much less rapidly toward the aperture. The shell is exogastric, but the living chamber is only slightly curved, in which it again differs from *E. micron.*

The failure of the ventral part of the aperture to be perfectly preserved leaves perhaps some basis for questioning whether this species might not better be placed in *Brevicoceras*. Although this feature is arbitrarily selected as the criterion between the two genera *Exocyrtoceras* and *Brevicoceras,* it is necessary to recognize that they were probably not well differentiated in Schoharie time, as shown not only by species in the Schoharie grit itself, but also by species in basal layers of the Onondaga limestone in western New York and in southern Ontario, which are almost certainly either contemporaneous with the Schoharie, or very close to it in time. These faunas are quite distinct in their cephalopods from those of the remainder of the Onondaga. The same horizon is clearly represented in the Eversole chert of the lower part of the Columbus limestone in Ohio, from which this species is derived. No cephalopods have been found which are common to the Eversole chert and the upper layers of the Columbus which yield a fauna of large brevicones and coiled cephalopods, comparable with the uppermost Onondaga faunas of western New York, and quite possibly contemporaneous with the Cherry Valley limestone of central New York.

Type.—Holotype, Ohio State University.

Occurrence.—From the Eversole chert member of the Columbus limestone, at Eversole Run, near Columbus, Ohio.

Hipparionoceras Flower, n. gen.

Genotype: *Hipparionoceras iowaense* Flower, n. sp.

This is a cyrtoconic shell which expands very rapidly to the aperture. The venter is less rapidly expanded than the dorsum, and the shell may therefore be considered an endogastric. The cross section is slightly depressed, the dorsum and venter equally rounded. The vertical profile is somewhat variable, but in general the ventral profile tends to be straight, while laterally and dorsally the shell expands so rapidly as to develop slightly concave lines. The sutures are essentially straight and transverse to the curving axis of the shell. The siphuncle lies close to the venter, and is composed of elongate segments, slightly longer than high, which are contracted abruptly at either end as they approach the septa, and are faintly scalariform in vertical section. No deposits are known in the camerae or siphuncle.

The surface is marked by transverse lines of growth, sometimes irregular and faintly rugose. These slope apicad on the siphonal side to form a hyponomic sinus.

Discussion.—In general aspect this genus is perhaps closest to typical *Conostichoceras* Foerste (1926) and *Turnoceras* Foerste (1926). Both genera, however, are definitely and even strongly exogastric, which this genus, though nearly straight, shows definite traces of slight endogastric curvature. Further, *Turnoceras* and *Conostichoceras* possess actinosiphonate deposits, and the segments of the siphuncle of those genera are unlike those of *Hipparionoceras* in outline. *Turnoceras* has concavosiphonate segments, while *Conostichoceras* possesses segments expanded at the apical end but conically contracted over the adoral end. Both genera further, are characterized by the flattening of the dorsum in cross section.

A few other genera are superficially similar. *Danaoceras* Foerste is a suberect rapidly expanding brevicone with an uncontracted aperture, but the section is compressed, and the siphuncle is actinosiphonate and is composed of more slender segments. *Codoceras* Foerste (1926) is definitely endogastric and rapidly expanding, but it has a large subcentral siphuncle. Both of these genera are typically Silurian, though *Danaoceras* has been recognized in the Devonian of Australia (Teichert, 1940), and the writer has subsequently been able to recognize the genus in the Middle Devonian of North America.

The lower Devonian *Herkimeroceras* Foerste (1926) is more slender than *Hipparionoceras,* is definitely exogastric, and has a small cyrtochoanitic actinosiphonate siphuncle. *Coelocyrtoceras* Foerste based upon *Cyrtoceras ventralisinuatum* Sandberger and Sandberger ,of the Middle Devonian of Germany, is perhaps closest of all the described genera to *Hipparionoceras.* It is an endogastric cyrtoconic genus, with the siphuncle and the hyponomic sinus on the concave side of the shell. However, it does not resemble the present genus at all closely, being a very slender shell. Further, the cyrtochoanitic segments of the siphuncle are occupied by well developed actinosiphonate deposits.

Hipparionoceras is apparently widespread in the Devonian. The genotype is from the Upper Devonian of Iowa, and was selected as the type of the genus largely because the condition of the siphuncle was known. *H. ichnoides* is from the Onondaga limestone, while *H. lairdi* occurs in the Conewango group of the Upper Devonian of Pennsylvania. In addition, *Hipparionoceras expansum* (Kindle, 1900, p. 734, pl. 26, fig. 1), represents the genus in the Jeffersonville limestone of Indiana. *Cyrtoceras miserum* Barrande, of the Middle Devonian G1 of Bohemia, appears from the original illustrations to be a typical representative of the genus, as is *Cyrtoceras apertum* Barrande, from the Middle Devonian horizon G3 of Bohemia. (Barrande, pls. 146, 156.)

The morphological relationship of this genus with other breviconic nautiloids is uncertain. Indeed, the relationships of practically all of the genera which exhibit some similarity to this one, and which have been discussed above, are also uncertain.

Hipparionoceras iowaense Flower, n. sp.

Plate 4, Figs. 1-2

The holotype is an incomplete shell, from which most of the dorsum has been removed by weathering. The section is circular at the base, with a diameter of 28 mm. In the 26 mm. of the phragmocone the shell expands to 40 mm., the measurement being oblique, and almost midway between the height and the width. Here the shell is evidently very slightly depressed in section. The shell expands rapidly to the aperture. The ventral profile is straight, but laterally the sides flare and are slightly concave. Probably the same condition holds for the dorsum.

The 26 mm. of the phragmocone consists of eleven camerae which increase in depth from 1 mm to 4 mm. The sutures are straight and transverse. The siphuncle is close to the ventral wall. As exposed at a break near the base of the living chamber, it is 4 mm in diameter and 1 mm. from the venter. In vertical section, the segments are flattened at the ends, truncated by the septa, and faintly scalariform. Expansion of the segment within the camerae is largely confined to its extremities, although the free part of the connecting ring is faintly convex throughout the middle part of its course. The septal necks, not clearly observed, are evidently short and recumbent or nearly so. No deposits occur in the siphuncle. The siphuncle expands rapidly in the length of the phragmocone. At the adoral end of the shell the segments expand from 2 mm. to 4 mm., parallel to the plane of the septum, and a marked area of adnation is developed at the adoral end of the segment on the dorsum, and at the adapical end of the segment on the venter. At the adapical end of the siphuncle there is a deposit of calcite on the dorsal side. This is irregular and almost certainly inorganic.

The surface bears faintly rugose transverse lines of growth, which slope downward on the ventral (siphonal) side forming a very clear hyponomic sinus.

Discussion.—This species, in spite of the incomplete condition of the type, has been selected as the type of the genus because it is the only one of the several known species which has yielded adequate information concerning its

siphuncle. It differs from the other species in its proportions, in particular in the straight rapidly expanding venter, and the slight lateral concave profiles. The left lateral part of the type is missing, but a restoration of its probable position is indicated on the accompanying illustration of the type as viewed from the venter.

Holotype.—U. S. National Museum.

Occurrence.—From the basal part of the Coralville limestone, Upper Devonian, Volga Valley railroad hill, NE. 1/4 Sec. 13, Center, Iowa, 93N-9W., near Roudalia, Iowa.

Hipparionoceras ichnoides Flower, n. sp.

Plate 5, Fig. 2

Only the living chamber of this species is known. Conch rapidly expanding, the sides straight to the aperture. Section slightly depressed. The living chamber increases from 33 mm and 37 mm. at its base to 65 mm. and 75 mm. at the aperture. It has a ventral length of 30 mm. and a dorsal length of 37 mm. The aperture is largely straight, but shows traces of a hyponomic sinus on the ventral side. The septum at the base of the living chamber is nearly flat. The suture is straight and transverse. The siphuncle is 4 mm. in diameter at the septal foramen, 5 mm. from the ventral wall of the shell. Its structure is unknown. The original surface pattern is obscured by vermicular markings. The sides of the living chamber, though essentially straight in profile, show the original form of the shell clearly. They diverge much more rapidly laterally than vertically, and the dorsum slopes outward orad much more rapidly than does the venter, the plane of the septum being taken for reference. Restoration of the outline on this basis, indicates that the complete shell was very slightly endogastric, though the extant portion shows only faint traces of curvature.

Discussion.—The very rapid expansion of the living chamber, the transverse condition of the sutures, and the very slight curvature serve to distinguish this form from *Hipparionoceras expansum* (Kindle) which is more similar to this form in size and general proportions than any other species. That form is larger, much more strongly curved, with the dorsum definitely convex, the venter markedly concave in profile, and is a more elongate and a much more gradually expanding species. *H. ichnoides,* by its rapid expansion, is more closely allied to *H. iowaense,* from which it differs in its larger size, more rapid expansion, and more depressed section, and *H. apertum* (Barrande), is more similar in rate of expansion, but smaller and more definitely curved.

Holotype.—Collection of the writer.

Occurrence.—From the Onondaga limestone, Lime Rock, Genesee County, New York.

Hipparionoceras expansum (Kindle)

Cyrtoceras expansum Kindle, 1900. Indiana Dep. Geol., Nat. Res., Ann. Rep., 25, p. 743, pl. 26, fig. 1.

Nephriticeras expansum Kindle and Miller, 1939, Geol. Soc. Amer., Special Papers, no. 23, p. 94.

This is a relatively large species, and one characterized by the relatively slender shell and the marked curvature of the conch. The siphuncle lies slightly farther from the venter than in the other known species of the genus, but in other respects the shell is typical. The reference of this species to *Nephriticeras* is rejected on the basis of a number of morphological features. The shell lacks the impressed zone found in all members of that genus. The siphuncle lies too far dorsad of the center of the shell to suggest either *Nephriticeras* or any of its relatives. Further, although the aperture is apparently complete or very nearly so, there is absolutely no indication of a hyponomic sinus on the outside of the coil. Kindle, in his description assumed that the shell was curved exogastrically. The opposite interpretation here adopted, is not definitely proved by the known specimens of this species, but its obviously close similarity to *Hipparionoceras* and the strong discordance of the features noted above with *Nephriticeras,* or indeed any of the Rhadinoceratidae, suggest both the present interpretation of orientation, and the generic position. The species is known only from the Jeffersonville limestone of Indiana. The holotype is from Bunker Hill, Indiana. One poorly preserved specimen in the collections of the University of Cincinnati Museum suggests the presence of this or a very similar species in the Columbus limestone of Ohio.

Hipparionoceras (?) lairdi Flower, n. sp.

Plate 5, Figs. 4-5

The holotype, the only known specimen, is a shell flattened vertically by pressure. The shell is nearly straight, but shows a faint endogastric curvature, if the venter is recognized as the siphonal side. The shell expands very rapidly. The extant part of the phragmocone increases in its present condition from 15 mm. and 3 mm. to 24 mm. and 11 mm. in a dorsal length of 9 mm. The living chamber increases to a width of 32 mm. and a height of 21 mm., with a ventral length of 15 mm. and a dorsal length of 19 mm.

The sutures are straight and transverse. The extant part of the phragmocone contains five camerae, the last three subequal in depth. The siphuncle is exposed on the venter by weathering. The segments are convex in outline, broader than long, a segment being 2 mm. and .8 mm, in length. No deposits can be recognized in the siphuncle, though its strong preservation suggests at least a thickening of the connecting rings.

The aperture slopes orad from dorsum to venter, but there is not a clearly defined hyponomic sinus. The surface shows numerous faint transverse lines of growth.

Discussion.—This species is worthy of note as the only rapidly expanding brevicone with an uncontracted aperture thus far recognized in the Conewango. The known features are consistent with those exhibited by the better known species of *Hipparionoceras,* except for the obscurity of the hyponomic sinus, and the species is placed in this genus with doubt largely in regard for the distorted nature of the holotype. The simple aperture approaches the condition of the Mississippian genus *Welleroceras,* but that genus has a central siphuncle, and it is unlikely that it is even closely related to *Hipparionoceras.*

Type.—Holotype, University of Cincinnati Museum.

Occurrence.—From the Watering Trough parvafacies of the Big Bend magnafacies of the Conewango group of the Upper Devonian. Collected by Dr. Wilson Laird, from a road cut on the north side of Route 40, in the southeast corner of North Union Township, 1½ miles N 50 W from Summit, Pennsylvania.

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N. Y. STATE MUSEUM,
ALBANY, N. Y.

Locomotion in the Fossil Vulture Teratornis

Harvey I. Fisher

Various parts of the skeleton of the large Pleistocene vulture, *Teratornis merriami,* have been found in deposits in the southern United States, from California to Florida, and in Mexico. Nowhere are the remains as numerous or as well preserved as in the asphalt deposits of Rancho La Brea in southern California. It was this abundance and preservation of entire bones that made possible this study of its locomotor apparatus. I am grateful to the Los Angeles County Museum, Los Angeles, California, for the use of its facilities and specimens.

Teratornis merriami has been placed in a family distinct from, and yet closely related to, the family Cathartidae, the New World vultures. Many of the bony parts, the synsacrum, tibiotarsus, tarsometatarsus, coracoid, ulna and metacarpus are typically cathartid with little except size to distinguish them from the Recent condors, *Vultur gryphus* and *Gymnogyps californianus.* The skull and sternum are not cathartid in character although there are points of resemblance. The humerus has several peculiarities not found in the New World vultures.

The gross similarities of certain wing elements of the tertatorn to those in the cathartids have led to the suggestion that *Teratornis* was similar in its flight pattern, that is, that it was chiefly a soaring bird. There are few specific features to uphold this contention. It is known that *Gymnogyps californianus,* the California Condor, on level ground must run or hop for several yards to gain enough momentum to lift its weight into the air. It also needs to flap several times as it leaves the ground. If *Teratornis* had a similar type of wing, its run for the takeoff must have been even longer because of its greater weight. However, we find that its wing was shorter in relation to its body weight (Table 1), and its legs were much shorter than in *Gymnogyps* (Table 9). Its leg bones are more delicate distally. With such poor adaptations for running, a long run for the takeoff would have been an arduous, if not impossible, task. It seems likely that *Teratornis* was able to leave the ground by use of its wings more easily than can the present California Condor.

Miller (The Birds of Rancho La Brea, Publ. 349, Carnegie Inst., Washington, 1925) has wondered how *Teratornis* with its weak legs, soaring wings and great weight took off from a level surface. Such a combination of characters and terrain would seem to make the takeoff almost impossible. One possibility is that *Teratornis* lived exclusively in areas of cliffs and slopes where easy travel downhill would be sufficient to gain speed for soaring flight; this appears unlikely. I think it more probable that *Teratornis* rose from the ground by vigorous flapping of its wings.

The body weight of the teratorn compared with that of any other flying bird must have been enormous. An attempt to get a gross estimate was made by determining the areas of the sternum and synsacrum in *Haliaëetus* and

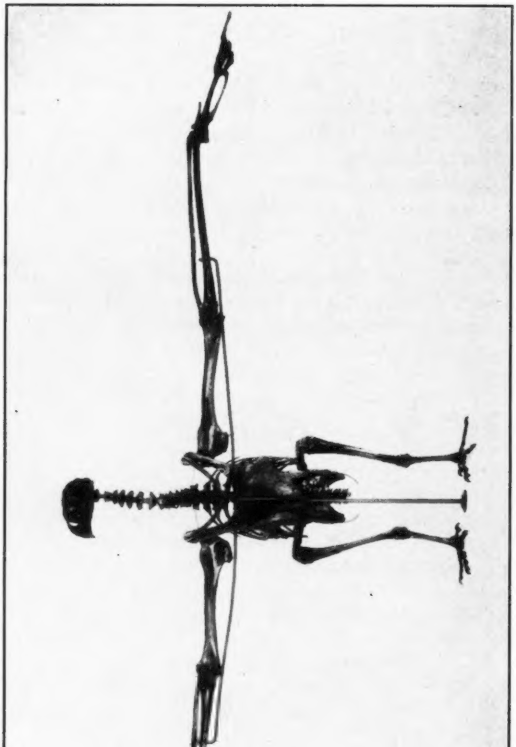

Fig. 1. *Teratornis merriami.* Wing spread (of bones), 7 feet, 3½ inches. In the Hancock Hall of Rancho La Brea Fossils. Courtesy of the Los Angeles County Museum.

Gymnogyps and comparing these areas with the known weights of the individuals measured. Thus if *Teratornis* had the same type of body build the areas of its sternum and synsacrum would furnish an index of weight. By this method the weight was found to be about 50 pounds.

Bones of the Wing and Pectoral Arch

Although the various bones of the wing were measured to determine the proportion of total wing length that each constituted (Table 1), the figures are useful only in a general way. The numbers of each element available differed and came from several tar pits so that the ratios derived from them must be viewed with caution when compared with ratios obtained from specimens in which the several elements belonged together.

TABLE 1.—Length in Millimeters of Bones of the Wing.

	Teratornis Minimum	*Teratornis* Average	*Teratornis* Maximum	*Gymnogyps* Average
Humerus	294	317	331	266
Ulna	404	421	430	308
Metacarpus	159	167	175	132
Digit II—Phalanx 1	59.6	64.9	68.7	53.2
Phalanx 2	49.4	54.0	58.7	43.9
Total	966	1024	1063	803

Length of Bones of Wing Expressed as Per Cent of Wing Length

	Teratornis Minimum	*Teratornis* Average	*Teratornis* Maximum	*Gymnogyps* Average
Humerus	30.6	30.9	31.1	33.1
Ulna	41.8	41.1	40.5	38.4
Metacarpus	16.5	16.3	16.4	16.4
Digit II	11.3	11.6	12.0	12.1

The ratios pertaining to proportions within the wing do not demonstrate any significant differences from those of *Vultur*, *Gymnogyps* or *Sarcoramphus*, except possibly a shorter humerus and a longer ulna in *Teratornis*.

Sternum.—There is nothing cathartid about this bony element, unless it be the number of costal facets for the articulation of the ribs (Fig. 1). Compared to any Recent New World vulture, the sternum is unusually wide (wider than long); the carina does not extend as far posteriorly, nor is it as high; the longitudinal axis of the row of costal facets (5 in number) is not parallel to the keel, the anterior end being produced laterally; the manubrium is greatly expanded laterally, and the keel is thicker but exhibits no such sudden broadening in any area as is found in *Gymnogyps*. The anterior and lateral margins of this bone are decidedly concave in *Teratornis;* in the California Condor the lateral edges are straight, and the anterior margin is sharply convex.

As discussed under M. supracoracoideus (p. 733), the muscle line separating this muscle from M. pectoralis superficialis has its posterior end swung medially to meet the middle of the length of the sternum in *Teratornis*. In

Gymnogyps the line never passes farther medially than two-thirds the width of the sternal plate on either side. This limitation of M. supracoracoideus to the anterointernal part of the sternum (compared with the cathartids) is not to be considered a factor limiting the ability to fly since it is similarly confined in *Accipiter, Falco* and *Pandion*, for example; this similarity may well be indicative of better ability to flap than is shown by modern vultures of the New World.

TABLE 2.—Measurements in Millimeters of the Coracoid.

	Teratornis			*Gymnogyps*	
	No. of Specimens	Avg.	Range	No. of Specimens	Avg.
Total length	13	164.4	155-174	8	108
Length sternal articulation	10	52.5	48.1-57.4	8	37.5
Least width below procoracoid	13	18.3	15.4-20.4	8	15.6
Anteroposterior thickness below procoracoid	13	13.4	11.0-15.3	9	10.9
Length of glenoid facet	13	38.6	36.9-41.1	9	29.7

Ratios Concerning the Coracoid

	Teratornis		*Gymnogyps*
	Average	Range	Average
Length sternal articulation: total length	31.8	29.9-35.0	34.7
Least width below procoracoid: total length	11.1	10.4-11.8	14.4
Thickness below procoracoid: total length	8.1	7.4-8.9	10.1
Length glenoid facet: total length	23.6	22.4-24.9	27.5

There is nothing further in the structure of the sternum to indicate that *Teratornis* was either a predominately flapping or a soaring type. The superficial resemblance of the sternum to that of *Diomedea* probably has little significance. The similarity is the result chiefly of the great width of the anterior end of the sternum in the albatross and the teratorn.

TABLE 3.—Measurements in Millimeters of the Scapula.

	Teratornis			*Gymnogyps*
	No. of Specimens	Average	Range	Average
Total length	5	153	141-160	114
Width in middle of shaft	4	13.1	11.9-15.1	10.0
Width: total length	..	8.6	7.8-9.8	8.8

The data in the second part of Table 4 demonstrate the difference in the proportions of the sternum between *Teratornis* and *Gymnogyps*. In the teratorn the anterior width is (relative to total length) twice as great, the intercostal width (between the most posterior facets) is much greater, but the relative posterior width is less than in the condor.

The relatively shorter, but higher carina (Table 4) in *Teratornis* more nearly approaches the condition found in some of the swift-flying, flapping hawks than it does in *Gymnogyps*.

TABLE 4.—Measurements in Millimeters of the Sternum.

	*Teratornis**	*Gymnogyps* Average of 6
Total length	165	156
Anterior width	170	74.4
Posterior width	97	81
Keel length	133	134
Keel height	53.4	33.3
Width through intercostals	117	71

* Only one sternum available.

Ratios Concerning the Sternum

	Teratornis	*Gymnogyps*
Anterior width: total length	103	47.7
Posterior width: total length	58.8	61.5
Keel length: total length	80.5	86.5
Keel height: keel length	40.2	24.7
Intercostal width: total length	70.9	45.5

Coracoid and furculum.—Essentially cathartid in pattern. The sternal end of the coracoid is relatively wider in *Teratornis,* and the clavicles join each other medially at less of an angle than in *Gymnogyps.*

TABLE 5.—Measurements in Millimeters of the Humerus of *Teratornis.*

	No. of Specimens	Average	Range
Total length	13	317	294-331
Proximal width	11	62.1	56.8-65.2
Distal width	12	60.0	55.2-63.6
Smallest diameter	11	19.6	17.7-21.5
Length bicipital crest	4	60.1	57.2-63.0
Length deltoid crest	16	125	117-132

Ratios Concerning the Humerus

	Teratornis Average	*Teratornis* Range	*Gymnogyps* Average
Proximal width: total length	19.4	19.1-20.0	18.7
Distal width: total length	18.9	18.1-19.3	17.6
Smallest diameter: total length	6.2	5.9-7.0	6.0
Length bicipital crest: total length	19.5	18.8-19.9	18.3
Length deltoid crest: total length	39.4	37.9-40.6	33.8

Although the coracoid in *Teratornis* is some 50 per cent longer than in *Gymnogyps* (Table 2), it is more slender in every respect.

Humerus.—This bone has been described by Miller (*op. cit.,* :90) who has pointed out a number of its unique characters. The ruggedness of the scars and impressions for the attachment of the heavy proximal musculature in *Teratornis* suggests a flapping mode of flight. Among Recent cathartids the form most frequently exhibiting flapping, *Coragyps,* shows a decided heaviness of the proximal muscles of the wing when compared to the extreme soaring type, *Gymnogyps.* Further, it is well known that locomotor extremities which are adapted for swift movement, the leg of the horse and the ostrich, for example, tend to have a decreased musculature distally and relatively heavier

muscles proximally. This reduces the work of the appendage by reducing the weight which must be moved through the arc described by the distal end of the wing or leg.

The long, inflated and elevated deltoid crest and the deep bicipital impression give additional support to the theory of a well developed proximal musculature in the teratorn. The elevated crest may be an important part of the mechanism for powerful rotation of the wing in flapping flight. Yet it must be remembered that the falcons, swift flyers that they are, do not show this particular modification. It is probable that they attain a similar mechanism, however, by extending the crest into a sharp point. Perhaps the width of the extended wing and the body weight are the differential factors here—relatively longer secondaries in *Teratornis* than in the falcons together with an undoubtedly heavier body may have necessitated this additional adaptation for successful flapping.

The ratios in Table 5 indicate that the humerus in *Teratornis* is stronger proximally, distally, and in its shaft. The bicipital crest is somewhat longer and the deltoid crest is significantly longer in the fossil. All these data add weight to the supposition that the proximal musculature of the wing was strongly developed.

Ulna.—There are few morphological characters, except size (Tables 1 and 6), to distinguish the ulnae of the condor and the teratorn. The ulna is relatively heavier distally in *Teratornis*, which may indicate an adaptation for flapping since the ratios of width to length approach the ratios for certain flapping hawks such as *Accipiter atricapillus* (Table 6).

TABLE 6.—Measurements in Millimeters of the Ulna in *Teratornis*.

	No. of specimens	Average	Range
Total length	3	421	404-430
Proximal width	4	41.6	39.9-43.1
Distal width	4	27.2	25.0-28.0
Smallest diameter	4	13.5	13.3-13.9

Ratios Concerning the Ulna

	Teratornis		*Gymnogyps*	*Accipiter atricapillus*
	Average	Range	Average	Average
Proximal width: total length	10.0	10.0	9.7	10.5
Distal width: total length	6.4	6.2-6.5	5.4	7.1
Smallest diameter: total length	3.25	3.2-3.3	....	.....

More secondaries were present in *Teratornis* than in modern *Gymnogyps* judging from the relative numbers of ulnar papillae (22 in *Teratornis* and 16-18 in *Gymnogyps*) and allowing for the fact that the number of tubercles is not an exact index to the number of secondaries. Although the papillae for the secondaries are somewhat larger and farther apart than in the California Condor, they do not appear to be as far apart relatively in *Teratornis*. If the feathers were similarly constructed in the two forms, this would seem to indicate lesser development of the secondaries in *Teratornis*, which in the vultures suggests a greater proclivity toward the flapping type of flight.

TABLE 7.—Measurements in Millimeters of the Metacarpus of *Teratornis*.

	No. of specimens	Average	Range
Total length	32	167	159-175
Least diameter second metacarpal	31	9.8	8.9-10.7
Distance proximal to extensor process	11	23.6	21.0-25.6

Ratios Concerning the Metacarpus

	Teratornis		*Gymnogyps*
	Average	Range	Average
Diameter metacarpal II: total length	5.9	5.3-6.4	9.6
Distance proximal to extensor process: total length	14.1	13.3-15.0	14.3

Carpometacarpus.—The shafts of the metacarpals, especially the third, are slimmer in absolute measurements in *Teratornis* than in *Gymnogyps*, but the overall length is greater! Thus metacarpal II is relatively only half as heavy as in the condor (Table 7). The proximal end of the metacarpus is heavier in the fossil, but the distal ends are the same absolute size. Thus this element shows the decrease in distal weight, and the entire bone is not as heavy relatively as in the condor. There is no difference in the length or the placement of the extensor process on metacarpal I.

TABLE 8.—Measurements in Millimeters of the Phalanges of the Wing in *Teratornis*.

	No. of specimens	Average	Range
Digit I, length	4	49.4	45.4-52.6
Digit II			
Phalanx 1, length	58	64.9	59.6-68.7
Phalanx 2, length	17	54.0	49.4-58.7
Digit III, length	11	39.5	36.1-44.0

Thus, the bones of the wing indicate relatively great strength proximally and a distal slimness which approaches the condition found in the falcons. Especially is this slenderness noticeable in the distal part of the ulnar shaft (not the distal articulation), the metacarpals and the phalanges. This is quite in contrast to the stocky, distal elements in the related cathartids which are soarers for the most part. The relative weakness of the bony tip of the wing leads to the tentative conclusion that the remiges in this region may have been less developed. The wing may have had short primaries and short distal secondaries, producing a rounded tip; or, the wing may have been more pointed than in Recent vultures. Either suggestion is indicative of a modification better adapted to flapping flight.

The bones also reveal strong muscle attachments proximally and weaker insertions distally. This again is indicative of an adaptation for a flapping mode of flight.

Muscles of the Wing

In any study of muscles made only by studying the muscle scars on the bones it is obvious that minor differences in attachments may be overlooked and that no data may be obtained on muscles which attach to other muscles or to ligaments. A further difficulty is that the only possible criterion for the

development of the muscles is the relative size of the areas of origin and insertion. Large muscles attaching by ligaments may differ greatly in their power-potential and this difference may not be reflected on the bone. In spite of these difficulties, it is practical and worthwhile to study the muscles "from the bones."

Throughout the myological part of this work *Teratornis* has been compared with *Gymnogyps californianus*, two specimens of which have been dissected.

It was possible to distinguish either the origin or the insertion, or both, of a number of muscles in *Teratornis* that showed no difference from those in *Gymnogyps*. These muscles are: M. coracobrachialis anterior, M. proscapulohumeralis, M. subscapularis, M. dorsalis scapulae, M. subcoracoideus, M. biceps, M. triceps, M. flexor metacarpi radialis, and M. extensor pollicis longus. This, of course, does not mean that the muscles are identical in the two genera.

M. pectoralis superficialis. Superficial Layer.—The area of origin in *Teratornis* is much more extensive; it includes approximately three-fourths to four-fifths of the ventral surface of the plate of the sternum, in contrast to less than 50 percent of this area in *Gymnogyps*. In the California Condor there is also extensive origin from the ventral ends of ribs 4, 5 and 6. The origin from the ventral edge of the carina is apparently similar in the two genera, as is that from the furculum. On the sternal plate in *Gymnogyps* the area of origin is approximately 24 square centimeters; in *Teratornis* it is almost 90 square centimeters.

Comparison of the wing lengths shows that the wing in *Teratornis* is only 25 per cent longer than in the Recent condor; thus the origin of this muscle is much larger in relation to wing length in the fossil form. Study of the various skeletal elements leads one to believe that *Teratornis* weighed at least twice as much as *Gymnogyps*. Consequently, the origin is also large in relation to body weight.

The areas of insertion of the superficial layer of M. pectoralis superficialis are approximately the same absolute size! In *Teratornis* the scar is 29.8 per cent as long as the humerus. It is 36.5 per cent in *Gymnogyps*. Nor is there any difference in the placement, longitudinally on the humerus, of this part of the pectoral musculature. The important difference in the insertion is the high, rolled condition of the distal half of the deltoid crest in *Teratornis*. The greater height and more medial situation of the insertion in the fossil make the muscle more efficient in rotating the wing.

M. pectoralis superficialis. Deep layer.—The extent of the origin of this layer from the carina is much more limited in *Teratornis* than in *Gymnogyps*, but in the former the origin extends laterally on to the ventral surface of the sternal plate. As a result the origin is relatively larger in the fossil, but is more posteriorly and laterally situated.

The insertion of the deep layer is on an elongate papilla in *Gymnogyps*, some 44 per cent of the way distally on the humerus. In *Teratornis* the area of insertion is a relatively larger, raised ridge, about 41 per cent of the way distally on the humerus.

The chief function of these two layers of the pectoral muscles is depression of the entire wing and depression of the leading edge of the wing. These actions are especially important in flapping flight, where the anterior edge of the wing must cleave the air cleanly and allow no escape of air forward from beneath the wing. Depression of the anterior edge at the outset of the downstroke accomplishes this. In the later phases of the stroke, the action of these muscles in pulling the wing posteriorly against the mass of air gives forward motion to the body.

In soaring or sailing, rotatory movements of the entire wing are often slight. Depression of the anterior edge of the wing is the only rotatory movement accomplished by M. pectoralis superficialis, and in soaring this particular rotation is perhaps almost automatically produced to excess by the upward force of air beneath the long lever arms of the secondary flight feathers which form the main support for the weight of the bird. Consequently, it may be assumed that when the bird is soaring this muscle operates chiefly to hold the whole wing down.

The greater size relatively of the superficial and deep layers in *Teratornis* as judged by the areas of origin makes it better able to depress the wings in flapping flight and to hold them down horizontally in soaring. The shorter work arm in the fossil genus, as represented by the more proximal insertion on the humerus, does not, I believe, offset the efficacy of the larger muscles. An unknown, but important, factor here is the length of the remiges. If they were relatively longer than in *Gymnogyps,* the differences discussed above are further minimized.

M. supracoracoideus.—The origin of this muscle from the sternum is actually smaller than in *Gymnogyps.* It does not extend posteriorly to the end of the keel as in the California Condor and is limited on the plate to the antero-internal corner. On the coracoid the origin in *Teratornis* covers less than the medial half of the basal width; in *Gymnogyps* the origin covers more than two-thirds of the anterior face of the coracoid.

The insertion is similar in the two genera.

There seems to be no doubt that M. supracoracoideus is weaker in *Teratornis* than in *Gymnogyps.* This weakness probably resulted in decreased ability to flap the wings rapidly and in decreased maneuverability in soaring since it is the important muscle functioning to raise the wing. In slow flapping, however, lesser ability to raise the wing is not disadvantageous for the weight of the body hanging on outstretched wings automatically raises them to a position for the beginning of the next stroke. In soaring, the weakness of this muscle probably is not a serious limitation since many of the small, delicate rotations and elevations of the proximal part of the wing could be performed by the shoulder muscles originating from the scapula and the vertebral column.

In at least one way the M. supracoracoideus is more favorably situated in the teratorn than in *Gymnogyps;* it originates farther forward in *Teratornis.* This enables its tendon to pass dorsally through the triosseal canal to the humerus at a lesser angle to the main body of the muscle. This would increase the efficiency of the muscle by increasing the vector of effective force and decreasing the vector of force wasted in end thrust on the bones of the canal.

Although this shorter muscle in *Teratornis* may have been able to exert its pull more directly on the humerus, its very shortness gives rise to another weakness. M. supracoracoideus in the California Condor is a long, somewhat thin muscle adapted to pull its point of insertion a relatively long distance; that is, to elevate the humerus some distance. The shortness in *Teratornis* decreases the distance through which the point of insertion is moved, and thus might limit the elevation of the wing when used in flight. It must be considered, however, that extreme elevation is perhaps never brought about by M. supracoracoideus alone. The shoulder muscles, Mm. rhomboideus, latissimus, deltoideus and dorsalis scapulae, probably bring the wing to the vertical position often seen in feeding or fighting vultures.

The functions in various types of flight and the interrelationships of Mm. pectoralis, supracoracoideus and coracobrachialis posterior (pectoralis tertius) are so little understood that generalizing from dissections and especially from the position of the anterior intermuscular line on the coracoid may lead to dubious results. Limitation of the origin of M. supracoracoideus to the anteromedial part of the sternum might be considered a weakness in *Teratornis*, as compared with *Gymnogyps*, but a brief survey revealed that the relative size of the attachment area and its position on the sternum in this fossil could be duplicated many times in other falconiforms—*Aquila, Uroaëtus, Accipiter, Buteo, Haliaëetus, Circus* and *Falco,* for example. Because of this similarity to forms which must be considered better flappers than *Gymnogyps,* and in spite of the relative smallness of the origin of the muscle in *Teratornis* as compared with *Gymnogyps,* M. supracoracoideus in the fossil form was probably better adapted to flapping than it is in the California Condor.

The position of the intermuscular line on the coracoid has been for some time considered an index to the "flying ability" of a bird by indicating relative development of M. supracoracoideus and M. coracobrachialis posterior. Yet, according to this index *Accipiter* has less "flying ability" than *Cathartes,* and *Nettion* less than *Coragyps* (Fisher, Auk, 62:125-129). The line on the coracoid in *Teratornis* is more like the accipitrine than like the cathartid. There is much to learn about the interactions and coactions of muscles before one can state with any degree of assurance their relative values in any type of flight or ground locomotion.

M. latissimus dorsi.—Although the insertion on the humerus has the same relative length of power arm for humeral flexion in the two genera, in *Teratornis* the line of insertion is relatively longer (16 per cent of humeral length compared with 10 per cent in *Gymnogyps*). This may indicate a stronger M. latissimus.

When the humeri of the two forms are laid side by side, it may be noticed that the line of insertion is farther forward on the humeral shaft and more nearly parallel to the shaft in *Teratornis.* This anterior insertion which is situated on a low ridge provides a better lever to elevate the leading edge of the wing in soaring flight or in the major rotation in flapping flight.

The stronger muscle for flexing the humerus and the better mechanism for elevating the anterior edge of the wing in *Teratornis* indicate greater ability to move the wing through the motions accompanying flapping flight. Although

the same motions occur in soaring flight, strong flexion of the humerus is much more limited.

M. latissimus dorsi is an important muscle in holding the flexed wing up against the body as in a perched bird. It seems unlikely, however, that the larger muscle in *Teratornis* is a result of this use, since the wing (exclusive of feathers) is not proportionately as long as in *Gymnogyps*.

M. deltoideus minor.—The origin is the same in the two forms. The insertion in *Teratornis* is in the same position as in *Gymnogyps* but is situated on a higher deltoid ridge. It is smaller in area by one-fourth in the teratorn.

It is impossible to determine the effect of a smaller muscle and a longer lever arm in *Teratornis*, compared to a larger muscle and a shorter lever arm in *Gymnogyps*. If the mechanism is less effective in *Teratornis*, it probably results in lesser ability to flap since M. deltoideus minor simultaneously elevates the humerus, pulls it anteriorly and elevates the leading edge of the wing —movements which occur in the recovery stroke of the wing.

M. deltoideus major.—The insertion in *Teratornis* is wider proximally but is the same absolute length as in *Gymnogyps*. Thus it is much shorter relatively; it does not extend past the distal end of the deltoid crest as it does in the condor. Further, there is no scar indicating another, more distal, insertion which is present in *Gymnogyps*.

Consequently it must be granted that the movements resulting from the action of M. deltoideus major are weaker than in *Gymnogyps;* those movements are the same as described for M. deltoideus minor except that flexion of the humerus is a more important function in the major deltoid. The absence of the distal insertion in *Teratornis* reduces greatly the power to flex the humerus.

M. biceps.—The power arm of this muscle is the same relative length in the condor and the teratorn, judging from the points of insertion. No differences in size of the areas of insertion were found.

M. triceps.—No differences were noted.

M. brachialis.—Both the origin and the insertion are relatively larger in *Teratornis*. The impression of the origin on the humerus lies at more of an angle with the long axis of the humerus—the proximal end is farther posteriorly, and the entire scar is more proximal than in the California Condor.

The large impressions indicate better development of M. brachialis. The more proximal origin in *Teratornis* together with the same points of insertion as in *Gymnogyps* indicates a longer muscle in the fossil; the higher area of origin also increases the efficiency of the muscle by decreasing the end thrust of the ulna and radius on the humerus.

M. anconeus.—Development and lever arms similar in the two genera.

Greater development of the proximal wing musculature, relatively reduced distal musculature (as judged from bones), a heavy, strong humerus and weaker distally bony elements in *Teratornis*, as compared to *Gymnogyps*, indicate a

mechanism better adapted for flapping flight. Most probably the flight pattern in flapping was similar to that in modern herons and pelicans, a slow, strong stroke of rather limited extent. No doubt the teratorn could also soar efficiently, but its relatively short wings and heavy body must have limited the use of soaring to times and areas of strong winds and updrafts. This combination of characters would have made "impossible" its soaring under conditions in which *Gymnogyps*, and especially *Cathartes*, can soar indefinitely.

Bones of the Pelvis and Hind Limb

Synsacrum.—Although this bony part is slightly longer in *Teratornis* than in *Gymnogyps*, it is some 40 per cent wider in the teratorn. The angle between the long axes of the preacetabular ilium and the postacetabular ilium is the same in the two forms. This would indicate similar use of the hind limb and also reveals the improbability that *Teratornis* ever used the limb in grasping or in predation. In hawks and owls which use the hind limb for specialized grasping the postacetabular part of the synsacrum is depressed more sharply. The advantage of this may be found in the fact that postfemoral muscles arising from this part of the pelvis are brought into a more advantageous position for movement of the leg; their long axes are more nearly parallel to the desired vector of force.

TABLE 9.—Lengths of the Bones of the Leg in Millimeters.

	Teratornis			*Gymnogyps*
	Minimum	Average	Maximum	Average
Femur	144	151	160	139
Tibiotarsus	215	227	238	210
Tarsometatarsus	133	138	148	115
Digit III				
Phalanx 1	38.9	43.1	47.7	42.5
Phalanx 2	27.8	30.5	32.7	30.8
Phalanx 3	25.0	28.2	31.6	26.4
Phalanx 4	25.3	28.1	29.6	27.5
Total	609	646	688	591.2

Length of Bones of Leg Expressed in Per Cent of Leg Length

	Teratornis			*Gymnogyps*
	Minimum	Average	Maximum	Average
Femur	23.7	23.4	23.3	23.7
Tibiotarsus	35.4	35.1	34.6	35.9
Tarsometatarsus	21.8	21.4	21.5	19.6
Digit III	19.2	20.1	20.6	21.7

Although such depression may improve the efficacy of the predatory mechanism, it reduces the extent to which the leg may be moved anteroposteriorly since the postfemoral muscles are shorter and the postacetabular ilium restricts the movement posteriorly. In forms specialized for swift locomotion on the ground, the road-runners (*Geococcyx*), for example, the parts of the synsacrum are in practically a straight line, and the fossa for the postfemoral muscles is enormously enlarged.

Some swift runners, *Oreortyx* and *Lophortyx*, for example, exhibit some depression of the posterior part of the synsacrum, but again the postfemoral musculature arises from relatively deep, ilial fossae.

These comparisons demonstrate the absence of specialization in the pelvic part of the hind limb mechanism in *Teratornis*. The synsacrum is typically cathartid and reveals that the teratorn was a heavy-bodied bird. This vulture is undoubtedly the heaviest form known to fly.

Femur.—The most striking features of this bone in *Teratornis* are its straightness in lateral view, its heaviness, and its shortness when compared to *Gymnogyps californianus*.

TABLE 10.—Measurements in Millimeters of Femur of *Teratornis*.

	No. of specimens	Average	Range
Total length	18	151	144-160
Proximal width	17	38.1	34.7-42.8
Distal width	14	39.0	36.1-41.0
Smallest diameter	17	17.9	17.3-19.2

Ratios Concerning the Femur

	Teratornis Average	*Teratornis* Range	*Gymnogyps* Average
Proximal width: total length	25.3	22.7-27.0	22.7
Distal width: total length	25.9	24.5-27.0	25.1
Smallest diameter: total length	11.9	11.2-12.7	11.3

In lateral view the femur is a straight column with somewhat enlarged ends, but in anterior view the lateral condyle appears to have lengthened and enlarged, which pushed the distal end of the rotular groove medially. The result of this is that the rotular groove in *Teratornis* is bent medially to a greater extent than in *Gymnogyps* and this in turn throws the lower leg in under the body farther. This modification may occur as a compensatory adaptation to counteract the straddling movement of the limb which would result from the wide separation of the femora where they attach to the wide synsacrum. The synsacrum being narrower in *Gymnogyps* and the legs relatively longer, there is lesser need for such adaptation.

The shaft of the femur appears heavier in relation to its length in *Teratornis* and the extremities are less defined. The neck is hardly discernible, and the distal areas of muscle attachment, especially the popliteal, are less developed and are relatively smaller.

TABLE 11.—Measurements in Millimeters of Tibiotarsus of *Teratornis*.

	No. of specimens	Average	Range
Total length	15	227	215-238
Proximal width	15	29.0	26.6-31.2
Distal width	15	27.7	25.9-29.2
Length fibular crest	15	50.4	44.1-58.3

Ratios Concerning the Tibiotarsus

	Teratornis Average	*Teratornis* Range	*Gymnogyps* Average
Proximal width: total length	12.7	11.6-13.5	13.0
Distal width: total length	12.1	11.5-12.9	11.6
Length fibular crest: total length	22.1	18.8-26.1	21.5

The whole aspect of the femur is reminiscent of a graviportal type of locomotion which would be in keeping with the great weight of *Teratornis*.

Tibiotarsus.—The tibia, like the femur, is stockier than in *Gymnogyps.* All the cnemial crests are less developed in *Teratornis* and the fibular crest is lower but wider and heavier. In relation to total length the articular surfaces at either end are broader and flatter in the teratorn, another indication of lesser mobility in the hind limb.

Tarsometatarsus.—The proportions within the tarsus are nearly the same in the two genera. There is some indication of a lesser trochlear width in *Teratornis,* and the shaft is thicker and slightly narrower than in *Gymnogyps.*

TABLE 12.—Measurements in Millimeters of Tarsometatarsus of *Teratornis.*

	No. of specimens	Average	Range
Total length	116	138	126-148
Proximal width	29	32.5	30.7-34.0
Distal width	27	33.0	31.0-34.7
Distance proximal to tibialis insertion	30	25.3	23.0-26.6
Least transverse diameter of shaft	28	14.3	13.0-15.6
Sagittal diameter middle of shaft	28	12.3	10.9-13.4
Transverse diameter third trochlea	27	12.7	12.1-13.3
Sagittal diameter third trochlea	28	20.5	19.2-21.6
Greatest sagittal diameter of head	26	27.4	25.3-29.3

The proximal surface of the tarsus is flatter and the intercotylar prominence is weaker in the teratorn. Digit I is relatively larger and situated more distally, judging from the articular facet on the tarsus. Further, it was more posteriorly situated in the fossil form. Digit II was rotated inwardly and posteriorly to a greater degree than in *Gymnogyps.* Digit III occupies the same position in the two forms, but digit IV seems to be more laterally directed in *Teratornis.* The effect of these rotations and of the more distal position on the tarsus of the articulating areas of digits I and II is to make a wider base for better balance of the heavy body and to distribute the weight more evenly on the several digits. In spite of these modifications the foot of *Teratornis* is relatively narrower, at least at the basal end of the toes.

TABLE 13.—Ratios Concerning the Tarsometatarsus.

	Teratornis Average	*Teratornis* Range	*Gymnogyps* Average	Type of *Cathartornis gracilis*	Type of *Sarcoramphus clarki*
Transverse diameter of head: total length	23.3	22.5-25.3	23.1	22.4	21.5
Sagittal diameter of head: total length	19.5	18.2-20.7	18.2	18.8	18.0
Trochlear width: total length	23.6	22.6-24.9	25.6	......	23.6
Transverse diameter of shaft: total length	10.15	9.43-11.7	11.9	8.50	9.80
Sagittal diameter of shaft: total length	8.8	8.4-9.8	7.82	8.65	7.9
Transverse diameter trochlea III: total length	9.1	8.5-9.3	9.82	8.95	9.5
Sagittal diameter trochlea III: total length	14.3	13.1-15.1	13.6	14.6	13.3
Transverse diameter trochlea III: sagittal diameter	63.5	60.2-67.2	72.4	61.3	71.6

Except for its slenderness as compared to more proximal parts of the hind limb the tarsus supports the suggestion that *Teratornis* tended more toward graviportal support of the body than do the Recent cathartids.

There is little evidence in the proportions of lengths of digits to length of leg that the digits were shorter in *Teratornis* (Table 14). However, it must be remembered that the leg in the teratorn is much shorter than in *Gymnogyps* in relation to body weight and wing length. Thus the digits are also short in relation to body weight and wing length.

TABLE 14.—Measurements in Millimeters of the Phalanges of the Foot.

	No. of specimens	*Teratornis* Average	*Teratornis* Range	*Gymnogyps* Average
Digit I				
Phalanx 1	16	23.4	21.3-24.3	23.6
Phalanx 2	9	26.5	25.5-28.8	17.9
Total length		49.9	46.8-53.1	41.5
Digit II				
Phalanx 1	36	26.7	24.1-30.1	30.6
Phalanx 2	33	24.0	21.0-27.1	24.8
Phalanx 3	14	28.3	26.3-31.2	25.3
Total length		79.0	71.4-88.4	80.7
Digit III				
Phalanx 1	38	43.1	38.9-47.7	42.5
Phalanx 2	38	30.5	27.8-32.7	30.8
Phalanx 3	34	28.2	25.0-31.6	26.4
Phalanx 4	8	28.1	25.3-29.6	27.5
Total length		129.9	117.0-141.6	127.2
Digit IV				
Phalanx 5	7	21.7	19.2-24.5	21.5

Ratios Concerning Phalanges of the Foot

	Teratornis Average	*Teratornis* Range	*Gymnogyps* Average
Length digit I: leg length	7.71	7.25-8.21	7.02
Length digit II: leg length	12.22	11.06-13.66	13.67
Length digit III: leg length	20.1	18.1-21.9	21.55

There is nothing in the bones of the hind limb to indicate that *Teratornis* was agile on the ground. The short leg, the columnar character of all the elements in the limb, the absence of well developed crests and attachments for large muscles, the flatness and relatively large size of the articulating surfaces, combined with the great body weight necessitate the theory that *Teratornis* moved ponderously on the ground. Certainly it was not even as adept on the ground as the California Condor which is perhaps the least agile of North American cathartids.

Muscles of the Hind Limb

Fewer differences were found between the condor and the teratorn in the muscles of the leg than were exhibited by the wing musculature. Part of this is due to the inability to differentiate individual attachments on the distal end of the femur and the area of the cnemial crest of the tibiotarsus. Another factor is the origin by thin tendons and by aponeuroses from the synsacrum of several important muscles. Many significant differences may be hidden in these "'illeg-

ible" areas, as well as in the attachments to the phalanges of the foot, which it was impractical to study.

However, a better explanation of lesser difference in the myology of the leg may be found in the use of this limb. In the New World vultures the feet have no grasping power and are not used in predation, and the various species are rather awkward on the ground as compared to related hawks. The legs are used simply as supports on the ground and on large limbs when the bird is perched. Little time is spent on the ground. The wings are the means of movement to and from food and they also constitute the chief mechanism for protection of the individual. Under such conditions it seems probable that selection would operate more effectively in regard to changes in the wing and thus tend to accumulate certain adaptive modifications more rapidly.

M. extensor iliotibialis lateralis.—Although the regions of attachment of this muscle are not discernible on the bones, if it inserted on the tibial crest as in *Gymnogyps* the lever arm must have been relatively shorter in *Teratornis* because the cnemial crest is not thrust as far anteriorly in this genus. This weakness would result in lesser ability to extend the tibia, and consequently the lower leg.

M. gluteus profundus.—The fossa for the origin is relatively small in *Teratornis;* actually it is about the same length in the two forms but is wider in the teratorn. This shortness in the fossil is a disadvantage in that the arc through which the femur may be pulled forward must be relatively shorter than in the California Condor. Then too, the insertion on the femur is more proximal, which shortens the lever arm in relation to the work arm. The shortness of the lever arm does not, however, affect the ability to rotate the outer surface of the femur forward and inward, which movement is important in bringing the lower leg beneath the weight of the body. The latter function probably is more important as regards this muscle.

M. iliacus.—The scar of insertion is large, indicating a more powerful muscle in *Teratornis* than in *Gymnogyps*, but the lever arm is some three per cent shorter in the fossil genus.

It is significant that these muscles which rotate the femur to bring the leg beneath the body are well developed in *Teratornis*, whereas muscles moving the femur anteroposteriorly seem weak. It indicates a limited length of stride but good ability to hold the legs in an optimal position for support of the body.

M. vastus lateralis.—In the teratorn the area of origin is relatively larger; it extends farther proximally and distally and extends more on to the posterior surface of the femur. The bluntness and weakness of the cnemial crest, its main insertion, reduces the efficacy of this powerful extensor by shortening the power arm.

M. vastus medialis.—The muscle is similar in the two genera, but its power of extension is even more reduced than in M. vastus lateralis by the vestigial condition of the cnemial crest.

M. flexor cruris medialis.—The insertion is no larger in absolute size than

in *Gymnogyps*. Further, it is on the middle of the medial side of the tibia and thus is less effective in rotating the lower leg into a position beneath the body. Its main function in *Teratornis* apparently was simple adduction and flexion of the tibia. The lever arms on the tibia are similar in length. In Recent cathartids the tendon of this muscle also attaches to the tendons of M. flexor cruris lateralis and M. gastrocnemius. Any weakness in M. flexor cruris medialis, such as is indicated by the small area of bony insertion, because of these additional insertions, reduces the ability to flex the shank and to extend the tarsus.

M. caudofemoralis. Pars caudofemoralis.—This muscle is absent in *Vultur*, *Gymnogyps* and *Sarcoramphus* but is seemingly well developed in *Teratornis*. The large area of insertion is in the same position as in *Coragyps* and *Cathartes*. There probably is little effect on terrestrial locomotion because of the small size of the muscle; the attachment to the tail is more than likely the functional insertion. The presence of M. caudofemoralis is of interest in that it shows some affinity of *Teratornis* to the small vulture line of the cathartids, that is, the group now represented by *Coragyps* and *Cathartes*.

M. flexor ischiofemoralis.—The fossa for its origin is relatively smaller and shallower, but part of the origin in Recent forms is by aponeurosis. Therefore, one can not be certain that the muscle is relatively smaller in *Teratornis*. Its power arm on the femur is three per cent longer and is more anteriorly situated in the fossil. Since the main function of this muscle is to rotate the outer surface of the femur posteriorly and medially, causing the bird to "toe out," the more anterior insertion is advantageous. The lever arm on the femur is too short in all the cathartids and *Teratornis* for much effective backward pull on the femur.

Mm. adductor superficialis and *adductor profundus.*—The superficial part of this muscle mass is similar in the condor and the teratorn, but the insertion is more proximal in *Teratornis*, which shortens the power arm and reduces its efficiency. The profundus muscle is larger than in *Gymnogyps* and has a similar insertion.

In the modern cathartids the chief function of these muscles is to move the femur posteriorly, but the deep position of the profundus part also causes femoral adduction. The shorter power arm of the superficial layer in *Teratornis* reduces the ability to pull the femur posteriorly but does not affect the power of adduction. The better developed profundus in the fossil indicates greater powers of adduction. Thus in these two muscles we find decreased ability for moving the femur along the longitudinal axis of the body but increased ability to pull the femur inward, toward this axis.

M. gastrocnemius. Pars interna.—The fossa for its origin from the medial face of the inner cnemial crest is shallower in *Teratornis* and does not extend as far laterally.

It is difficult to delimit the insertion of the main tendon of the gastrocnemius complex of muscles because of its sheathlike nature. It is possible to note, however, that the tendon of insertion is narrower in actual measurements in the fossil because the ridges on either side of the post-tarsal groove are closer

together. These ridges which are the lines of insertion appear to be less defined in *Teratornis*, perhaps revealing a weaker insertion.

Any debility in the gastrocnemius group of muscles is directly revealed in lesser power of ground locomotion since this group functions as the most powerful extensor of the tarsus and is effective in flexing the shank on the femur due to the origin from the femur of the pars externa and pars media muscles.

M. tibialis anterior.—The development of this great flexor of the tarsus may be correlated with ability to walk or run, ability to grasp with the foot as in perching or in predation, and with weight of the foot or of the entire body. In fact, it is impossible to define and distinguish individual adaptations.

The power arm, expressed in per cent of tarsal length, is 18.0 in *Teratornis* and 19.1 in *Gymnogyps*, but this slight difference may or may not be correlated with agility on the ground. *Coragyps* which is more adept in terrestrial locomotion than *Gymnogyps* has a power arm only 13.9 per cent as long as the tarsus. The power arm is relatively long in some predatory types such as *Pandion* (34 per cent), but in *Aquila* is only 23 per cent, or 4 per cent higher than in *Gymnogyps* which can grasp nothing.

Because the insertions on the phalanges of the toes could not be studied, only the origins of the short, tarsal musculature may be compared. The origins of M. extensor brevis digiti III, M. extensor hallucis longus, M. extensor brevis digiti IV, and M. flexor hallucis brevis are actually smaller in *Teratornis* than in *Gymnogyps*. If these muscles were smaller, there would be lesser ability to adjust the position of the individual digits, but the major movements of flexion and extension need not necessarily have been limited since these motions are controlled for the most part by long tendons from the more proximal musculature of the shank.

The heavy, columnar condition of the leg bones, the absence of well developed crests, the more distal articulations for digits I and II to distribute the body weight more evenly on all the digits, and the spreading of the digits into a wide foot for better support are all indications of adaptations to carry the weight of the body. None of these characteristics is to be found in swiftly running forms.

The musculature of the hind limb is not developed commensurately with the weight of the body as compared to *Gymnogyps*. The length of the stride is limited by short proximal muscles which are relatively small. The only part of the musculature that is as well or better developed than in the Recent condor is the group of muscles adducting the leg. This is yet another manifestation of probable awkwardness in terrestrial locomotion.

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The Wasp Chlorion laeviventris as a Natural Control of the Mormon Cricket

(Sphecidae; Hymenoptera: Tettigoniidae, Orthoptera)

Ira La Rivers

Introduction

The black cricket wasp, *Chlorion laeviventris* (Cresson) first came into official prominence as a control of the Mormon cricket (*Anabrus simplex* Haldeman) when it was observed in increasing numbers in the cricket fields of Montana in 1927 (Cowan 1929) (see distribution of these in Fig. 1). Since then, the wasp has been recorded from other portions of the range of the cricket, and increasing recognition given to its value as a natural control of the pest. However, the author knows of no investigations which have been conducted to determine in detail the relationship between the cricket and the

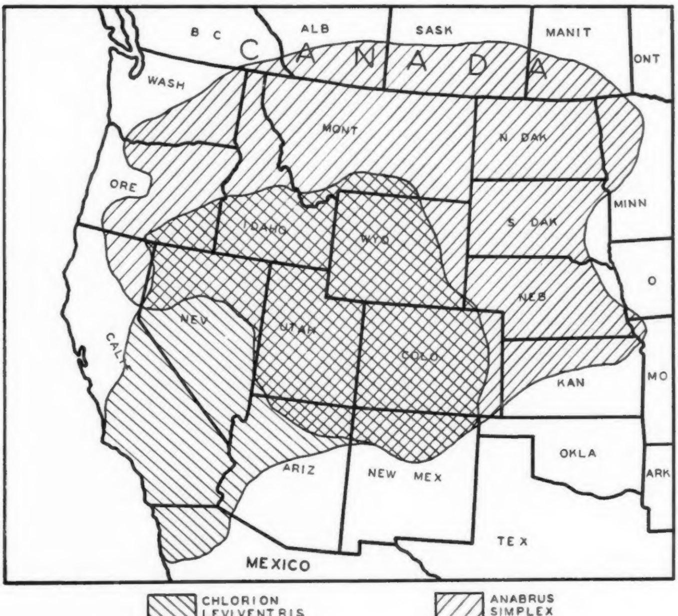

Fig. 1. Showing the approximate distribution of the Mormon cricket and the cricket wasp in western North America, and the regions where their ranges overlap.

wasp, and submits this report as a contribution toward a better understanding of the problem.

The area studied lies in the eastern foothills of the Bull Run Mountains, eight miles south-southeast of Mountain City, Elko County, Nevada, and is sagebrush country typical of the general habitat of the Mormon cricket. The district, containing some excellent farm lands along the Owyhee river, as well as superior open range in many sections, was suffering heavily, during the summer of 1939, from the depredations of several cricket bands (see Figs. 2 and 3). The author's fieldwork was accomplished while employed on the cricket control program, and during the time that conventional artificial control was practised to keep the insects from invading crop and grain fields, there were suitable opportunities to observe closely the effect of the parasitic wasp on concentrated numbers of crickets.

Observational Methods.—The infested area, a gently-sloping east ridge in the Bull Run mountains, was laid out in quadrats of decreasing size in order that tabulations of burrow concentrations could be made and an accurate estimate of the number of parasitized crickets arrived at (see Fig. 4). The invading cricket band was spread over a total area one mile long by one-half mile wide, and within this region three successively smaller quadrats were marked off and counting stations established. Each quadrat, from larger to smaller, was an area of progressively increasing cricket and wasp concentration. The respective divisions were designated: *Quadrat A*, the area as originally defined; *Quadrat B*, one-half by one-quarter mile, situated toward the northwest corner of *A*; *Quadrat C*, one-quarter by one-eighth mile, located in the

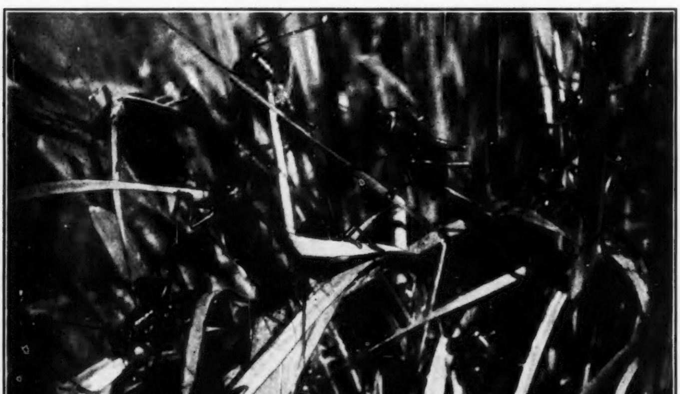

Fig. 2. Crickets feeding on Giant wild ryegrass *(Elymus condensatus)*. Note how the stems bend under the insects' weight. In many instances, crickets cause more damage to a hay meadow by this "trampling" of the grass than by their feeding.

northwest corner of B; and *Quadrat D*, an acre in the northwest corner of C, where the wasps and crickets were at maximum concentration.

One hundred and sixty-two counting stations, one square yard in area and placed approximately four yards apart, were established in *Quadrat D;* 242 counting stations, approximately twenty yards apart, permitted adequate sampling of *Quadrat C;* 313 stations, thirty-five yards apart, were placed in *Quadrat B;* while 465 stations, fifty feet apart, were utilized in *Quadrat A*.

Biologics

Each black wasp paralyzes a cricket by stinging it between the legs, then places the victim in a burrow, which may or may not be dug previous to the capture, generally adds a second victim to the burrow, deposits an egg on each cricket, and seals the burrow with the excavated soil. Several such burrows are dug, stocked, and closed by each wasp.

A. Digging the Burrow

On July 13, 1939, a large band of crickets appeared on the ridge, coming from higher ground to the southeast, and appearing first in greatest concentration on an alkaline area well up on the ridge, an area overgrown with stunted sagebrush *(Artemisia tridentata)*. At this point, observations of the wasp-cricket complex were initiated.

The morning after the crickets' appearance, the wasps were busy completing burrows, stocking them with paralyzed crickets, and closing them. Burrows were begun either late the preceding evening, or before dawn of that day, and stocked with crickets and closed by 8 and 9 a.m., the site of the closed nest marked by the characteristic, low mound of pebbles with which each wasp terminated her labors. Four days later, the wasp activity was approaching its minimum, but cricket invasions of the higher, western end of the ridge brought a new influx of wasps. Thus, six days after the appearance of the crickets, wasps were tunneling the entire upper length of the ridge.

Excavating Methods.—The author's inaugural acquaintance with the cricket wasp was in a slightly alkaline area on the eastern tip of the ridge. While walking through the brush after dark, a tremulous, persistent humming was heard. Following the sound, the source proved to be a large wasp digging her tunnel in the lightly-colored soil between two sagebushes. The time was 8:50 p.m., and an almost full moon and a flashlight aided observance of the wasp's work.

When first seen, she was working with only her head in the entrance. The tunnel had not yet taken shape, and the burrow was little more than a pit in the ground. At first, a steady arc of dirt was thrown backwards beneath the wasp by her rapidly-moving forelegs, and rapid progress was made. At 8:56, she had a considerable amount of refuse soil at the mouth of the now definite but short, tunnel, and she turned her attention to this. Here she bustled, and swept, and scraped, and smoothed until the earth lay freshly-strewn over an

Fig. 3. A female cricket climbing a stalk of ryegrass. A male clings to a stalk below her.

area of sixteen square inches. When this was completed to her satisfaction, she resumed work in the tunnel. By 9:08, the tunnel equalled her own length, and she could just be seen working in it. The soil seemed harder at this point, and progress slower. Several times she backed out of the burrow with hard soil fragments and pebbles in her jaws, and these were carefully carried several inches from the entrance and dropped.

Debris was never allowed to accumulate to the point of hampering the wasp's movements, and was swept out of the burrow as fast as possible, where it was scattered over the ground. Once, while tidying up about the entrance, she decided that a hitherto unnoticed quartz pebble half as bulky as herself must be moved to another spot. The rock was finally worried, rather than carried, to a position in the rear of the dump; each time the unwieldy burden slipped from her mandibles, the wasp hummed vigorously with her wings. However, further efforts to induce her to repeat the performance were in vain, and the pebble was ignored even when placed directly before the entrance. Perhaps had it been left there longer, she would have again hauled it away, but seeing that she went around it without attempting to remove it, it was replaced on the dump.

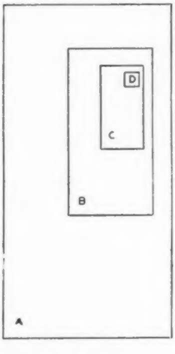

Fig. 4. Quadrats into which the infested ridge was divided to provide adequate means of sampling.

Again the wasp entered the tunnel. As she worked, her wings hummed periodically, and it was soon apparent that the sound of her wings was an approximate indication of the ease or difficulty of the work, for she was quiet when the soil was loose and easily worked, but began to hum softly when the labor grew more tedious, and once, when tearing at an unyielding bit of pebble embedded in the wall of the burrow, the sound of her wings rose to an unmistakably agitated buzz. This humming was confined to work in the nest except on two occasions, both involving the dragging of cumbersome pebbles away from the entrance.

The wasp worked continuously until 9:40, by which time she had lengthened the tunnel considerably. Mosquitoes and approaching cloudiness compelled a cessation of the observations, and a cyanide bottle was placed over the opening of the nest. Five minutes later, the stunned wasp was dug from the end of the twelve and one-half centimeter (five-inch) tunnel.

The average length of over 100 excavated nests was fourteen centimeters; over 65% of these contained two crickets, the first lying at an average distance of five cm. from the entrance and four cm. vertically below the surface, the second lying 9.5 cm. from the opening and seven cm. from the surface. The two burrows from which the *bona fide* four were taken (see below) were of approximately the same length, being 22 cm long, the first cricket lying seven cm. from the opening, and eight cm. below the surface, and last one occupying a position 18 cm. down the tunnel, and twelve cm. below the surface.

B. OBTAINING PREY

Upon completing the burrow, the wasp immediately starts in search of a cricket.

No Orientation Flight.—When leaving the tunnel, the wasp makes, in the author's experience, nothing comparable to the orientation flights recorded by the Peckhams (1898) for several allied species, and because of this, often gets into difficulty when the return trip is attempted (Fig. 5). Very rarely, individuals are seen to rest for a moment after the burrow is finished, but this is not a general habit. In searching for a victim, the wasp may fly several rods, or only a few feet—depending, apparently, upon the amount of energy the insect possesses for this particular activity. This supposition seems to be verified by the fact that a hunting wasp on a long flight may pass over several hundred easily accessible crickets before alighting in a clearing; and the flight may be for a distance of thirty yards or more, despite the fact that the clearing in which the burrow was made contained a number of moving crickets.

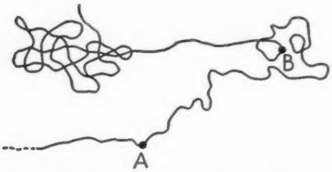

Fig. 5. Illustrating the unsuccessful attempt of a wasp to re-locate a cricket which was temporarily abandoned in the wasp's search for her burrow. At *A*, the wasp dropped the cricket she was dragging and flew in search of the burrow, which she finally located at *B*. But now she had lost the cricket! Not realizing that she had angled to the southeast in her search for the burrow, she persisted in looking for the cricket directly north of the burrow, and was finally forced to abandon the hunt. The paralyzed cricket was soon discovered by other crickets and eaten.

Overcoming the Cricket.—At 7:32 one morning, a wasp was watched overcoming a cricket. She alighted a few inches in front of the cricket, who made a half turn to the left before the wasp could catch him. She clung tenaciously to the hard thoracic shield of the cricket while his long hind legs tumbled them erratically over the ground. The wasp's abdomen was pressed tightly down along the victim's right side, the tip lying just beneath the right middle coxa, and between middle and hind legs. The sting could be seen just twice during the struggle, and was being plunged at the venter between legs. Once the cricket fell against a projecting sagebrush twig, pinning the wasp, who loosed her hold for an instant, then quickly regained it. At this point, the sting was seen to strike at the right side of the abdomen, about a quarter of an inch from the abdominal-thoracic juncture, but did not seem to penetrate.

After regaining position on the cricket's back, the wasp once more sought the ventral leg region with her sting, and quieted the victim within three seconds. The cricket lay on his left side, with only an occasional twitching of the tarsi to indicate he was still alive. The wasp did not immediately relinquish her hold, and inserted the sting twice more into the thoracic venter before resting. Then she moved nervously about near the cricket for several

seconds, then stopped beside it to rest. That the struggle had been strenuous for her was attested by the marked respiratory movements of the abdomen.

The sting effects a general paralysis of the ventral ganglia controlling walking activities of the cricket, but occasionally death results quickly from (1) too deep application of the sting, or (2) suffocation resulting from paralysis of the abdominal respiratory muscles, occasioned by a chance blow or two into the abdomen, or (3) both. The wasp is tenaciously persistent in striking for the victim's thoracic venter, but to one who has observed the struggle, it may be surprising at first that her percentage of successes stands as high as it does. Of 211 crickets taken from 109 burrows, only eighteen individuals were found prematurely dead from the effects of the sting. All crickets examined were taken from fresh burrows opened no later than four hours after closure by the wasp. This indicates a "paralyzing" efficiency in excess of 90%, allowing for the nominal margin of error. This in spite of the difficulty the wasp sometimes has in overcoming the victim.

Close observance of the contest brings two facts to light—(1) the wasp, while instinctively preferring to sting the thoracic venter of the cricket, very often pierces other portions of the victim's body during the struggle, and (2) a large number of stings are administered when the attack is hotly contested by the cricket, while fewer stings are given, generally, to a quieter victim.

Many wasps persistently strike at the ventral ganglia even while both contestants are rolling about on the ground, but others seem to sting wildly and promiscuously during the struggle, apparently trying to quiet the victim in order that a well-placed ventral thoracic sting—nearly always methodically given after the cricket has ceased to struggle violently—may be administered. It is not surprising, then, that the wasp should kill a cricket occasionally. However, this success is less striking when it is realized that the majority of stings given a cricket appear to be superficial, and not as damaging as would at first seem. As previously mentioned, death may result from deeper applications of the sting, but the relative activity of the wing muscles of exhumed male crickets is substantial evidence that the dorsal thoracic regions are generally unaffected, except for the secondary, milder, after-effects, for it is not uncommon for an otherwise completely paralyzed male to chirp shrilly when taken from a recently-completed burrow.

It is not yet known whether the death of the prey materially affects the attached wasp larva or not. Such an occurrence may be without any developmental significance whatsoever, for no one has proven (to the author's knowledge) that the larval wasp necessarily requires living food. It is a well-known fact that the poison injected by other species of solitary wasps acts antiseptically upon the carcasses of their victims, preserving them from decomposition for weeks, and insuring their progenies suitable food no matter whether the prey lives or dies. If the early death of the cricket is significant in this case, its effects probably appear as a stunting of the attendant larva, resulting in the emergence of a small wasp instead of a normal-sized one.

A Fly Parasite of the Cricket.—A third factor in the premature death

of the cricket is the occasional infection of adults with the large flesh fly *Sarcophaga tuberosa* Pand. Of the total of 27 dead crickets exhumed (see above), nine contained nearly grown larvae of this fly, and undoubtedly had been near death when taken by the wasp. The fly in turn is extensively preyed upon by the little bembicid wasp *Stictiella pulla* (Handlirsch) (La Rivers 1942).

The Cricket's Defense.—As previously indicated, the length and intensity of the struggle varies with both individuals involved, and while the author has never seen a wasp fail to subdue the cricket attacked, he has several times observed large and powerful crickets which were nearly successful in making their escape. The cricket, while lacking a weapon as formidable as the sting of the wasp, is not entirely defenseless, and has evolved pronounced protective reflexes. These consist of rolling over on either side, or balancing on head and a pair of legs while one or more legs are lifted to deliver a blow. The powerful hind legs are most often employed, but the insect may strike with any free leg. When it is remembered that the cricket may attain twice the length and four times the weight of the wasp, it can be readily seen that it is not entirely helpless. On the occasion in which the author noted the most nearly successful attempt of a cricket to defend himself, the hind legs were used. The wasp, blundering into these, was thrown two feet distant, and left momentarily stunned. Had the cricket moved on immediately, he would have escaped, but he remained motionless on his side, legs erect to deliver another blow, and was overcome by the quickly-recovering wasp.

Recognition of the Wasp as an Enemy.—At this point, it seems timely to review more fully the reactions of the cricket to the presence of the wasp. While on the ground, the marching cricket seems, in many instances, to be remarkably short-sighted in recognizing the wasp, even when she is energetically moving about, and will often deliberately move in her direction and touch her with its antennae before realizing the mistake.

As an example of this, as well as of the more or less inflexible character of the wasp's reflex chain, one morning northwesterly-migrating crickets were observed frequently interrupting a wasp who was busy closing her stocked nest. However, she showed no belligerence towards any of the passing crickets, some of whom were persistent in their annoyance. The busy wasp invariably drew the attention of passing crickets when they were within six or eight inches of her, and they quickened their pace, bent, no doubt, on investigating the possibilities of having discovered something edible. Not until they were in actual antennal contact did most of them realize their error. The effect was then ludicrous. They immediately assumed the defensive posture. Some rolled up on their heads, or over on their sides, hind and middle legs stiffly elevated; others merely raised one pair of legs. All remained motionless while the wasp went unconcernedly about her business. After a time, the crickets went on quickly. Once a cricket disturbed the wasp so that she flew off a distance of two feet to rest for a short time, flattened against the warm ground.

Toward a flying wasp, the crickets react quite differently. By far the greatest majority of them readily recognize the flying wasp as an enemy, and become defensively alert. A low-flying wasp will throw a clearing of migrating

crickets into confusion, some jumping erratically for cover, others rolling into the defense posture. There is strong doubt in the author's mind that the cricket takes the least cognizance of the sound of the wasp's wings, for his experience indicates that the crickets hear only a limited range of sounds, and these of wave lengths close to those which they themselves produce. Their sounds, restricted to the male, are shrill and high-pitched; so high-pitched, in fact, that many a time the author has listened to a male chirping in a bush and heard the sound fade in and out of perceptive range without noting any cessation of wing movements, indicating that some of the cacophany was beyond his ability to detect.

Talking or shouting will not disturb a migrating band of crickets, but sharp, piercing tones, such as are made when air is forcibly drawn in through the nose, or the squeak of tin against tin, will completely disorganize a clearing of symmetrically-migrating crickets. The drone of the wasp is relatively low-pitched, and while shrill sounds of a disturbing character can be detected by the crickets at distances of 40 or 50 feet, flying wasps are given no attention until they are within six or eight inches—that is, in actual visual range.

A band of crickets heavily preyed upon by the wasps often develops a strong degree of hypersensitivity to all similarly-sized objects-in-motion, and it is not uncommon to see one cricket assume the defensive when suddenly accosted by another cricket, especially in clearings where wasps are active, and contacts between wasp and cricket numerous. Under more normal conditions, where wasps were lacking, this reaction has not been noted.

C. THE TRIP BACK TO THE BURROW

Fly Parasites of the Wasp.—After quieting the cricket, the wasp rests a while. At this stage of the wasp-cricket relationship, nearly one-third of the observed flesh fly parasites of the wasp made their appearance. These tiny flies, representing the two species *Euaraba tergata* (Coquillet) and *Eumacronychia elita* Townsend, are striped light and dark grey, and vary from 3.75

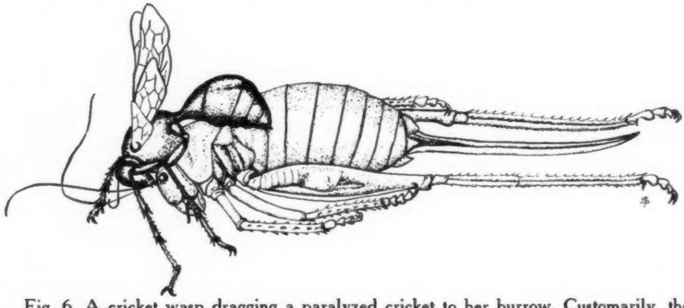

Fig. 6. A cricket wasp dragging a paralyzed cricket to her burrow. Customarily, the victim is grasped only at the base of the long antennae, but the wasp occasionally supplements this hold by taking the large, smooth head, or the neck, between her front legs, while some wasps use their wings to varying degrees to aid them with the heavy burden, especially over rough ground.

millimeters to 4.5 mm. in length. Against a light-to-medium colored soil, they are difficult to see, and it is generally their shadow that first attracts attention (La Rivers 1942). The flies, so similar in size and color as to be practically indistinguishable in the field, exhibit no fear of either the wasp or the cricket—and when present during the contest between the two, move about only sufficiently to keep out of the way. On more than one occasion, the author has seen a fly alight on a paralyzed cricket and minutely examine it while the wasp was resting. When the wasp starts off with her burden, the parasite accompanies them, sometimes flying ahead to wait on a twig, rock, or hump of ground, sometimes lagging behind, and less often, sitting on the cricket. In this manner the fly follows the wasp until the latter reaches her nest.

To drag the cricket, the wasp grasps the bases of the victim's antennae in her large jaws (Fig. 6), employing her wings occasionally to aid her where the ground is too rough or too soft for easy passage. When the burden catches on a projecting twig or hump of soil, the wasp often supplements her hold by grasping the cricket's head with her forelegs. Occasionally, during these trips back to the burrow, the wasp meets other foraging wasps, and is generally forced to fight for her prize. In nearly all such cases, the original owner is victorious; neither wasp ever seemed to be harmed during these encounters, and the loser goes on to search for another cricket.

Locating the Burrow.—The trip back to the nest is often the most crucial phase of the entire cycle. Several resting stops are generally made by the wasps, as well as usually one reconnaissance flight. The average distance that 68 wasps covered with their prey during the trip back to the nest was 23 feet, and this distance seemed to require an average of one reconnoitering flight for the wasp to orient herself. This flight usually took place at or beyond the halfway point; and after sighting familiar territory, the wasp returned to the cricket and dragged it the remaining distance without further delay. Wasps seemed to have considerable difficulty in finding their burrows when their prey was subdued 40 or more feet from the nest. The author recalls one energetic wasp who overpowered a cricket too far from her burrow. The trip back began at 8:45 a.m. After dragging the cricket a distance of one foot, the wasp rested for a minute, then proceeded. There followed then 100 feet of travel in eight minutes, the wasp making rapid progress over open, smooth ground, and having a difficult time getting through the cluttered debris between closely-growing bushes. At this point, the cricket was dropped, and the wasp flew off in search of the burrow. She located it 32 feet farther on, and after inspecting it thoroughly, flew back to find the cricket. The route she had followed with the cricket lay almost north and south. The nest itself was located—not in the direct line of march—but off to the southeast a distance of 18 feet directly east of the line of march. In attempting to retrace her flight back to the cricket, the wasp persisted in flying due north from the nest, and so consequently paralleled the real line of march, but never found it again. Meanwhile, six minutes after its abandonment, a cricket found the victim, and soon three others were contesting possession of it. The last to remain with the paralyzed cricket was the little parasitic flesh fly, who still hovered about when the author left.

Failure to Recognize Parasites.—Without exception, no wasp about which the little flesh flies were active seemed to be aware of the presence of the parasites. In this respect, this species of wasp seems less observant than related species. The Raus (1918), in reporting their observations of the large *Priononyx atrata* St. Fargeau, state that when a "little parasitic Dipteron" was hovering about the wasp, the latter would "whirl suddenly around, glare and jump at it defiantly, and it would dart away, only to return at once as teasingly as ever." And the Peckhams (1898) have this to say of *Pompilus scelestus* Cresson:

"While she was thus employed," (in digging the burrow) "the spider was attacked by a very tiny red ant, that could not by any possibility have stirred it. When the wasp caught sight of this insignificant marauder she fell into a fit of wild fury and bending her abdomen under, seized the ant again and again in her mandibles, and flung it backward against the tip of her sting. The little creature finally escaped, seeming none the worse for the rough handling to which it had been subjected, while the wasp, trembling with excitement, grasped her spider and rushed off to a distance of several feet, carrying it up on a weed and depositing it there."

D. AT THE BURROW

Attempted Crippling Of The Victim.—At the nest, the cricket is dragged into the tunnel, with or without a preliminary examination of the nest by the wasp. If the opening is large, the wasp carries the victim in just as she trekked with it, but if the tunnel is too small, she backs down it and drags her prey in by the long antennae. The cricket is generally placed in the tunnel headfirst, but occasionally one is found stuffed into a burrow tailfirst. Three minutes was the average length of time taken by the 82 wasps observed in this phase of their activities to deposit an egg on the cricket, and leave in search of a second victim. In several instances, five to six minutes elapsed before the wasp left the tunnel, and on one occasion, the insect remained in the nest for eight minutes. In all these cases, investigation of the cricket showed various mutilations of the legs. One such cricket, intact when brought into the nest, showed the following losses: on the right side—the first three protarsal segments, half of the mesofemur, and all of the metatibia; on the left side—the meso- and metatibiae were lacking. Since no case was observed in which the tunnel was too small to readily accommodate the victim, the Peckhamian assumption (referring to *Pompilus fuscipennis* St. Fargeau) that the habit "is related to the fact that she makes a very small nest in comparison to the size of her prey" is not applicable to this species. In fact, it is a matter of some doubt whether it is applicable to the case the Peckhams illustrated. A better interpretation of the significance of this act is Bouvier's suggestion, following Ferton, that the habit serves "only to render the inertia more complete." By crippling the victim, there is less danger that the egg or larva of the wasp can be jostled and harmed in the event the cricket actively revives after being placed in the nest and buried.

The single egg is attached to the base of the cricket's abdomen just above

the hind leg. There was no preference for either side, the side utilized depending entirely upon that which was most convenient to the wasp.

Eggless Wasps.—In excavating completed burrows, it was found that reasonable care had to be exercised in removing crickets to avoid losing the attached egg. Some eggs were securely glued to the victim's abdomen, while others seemed to have been poorly fastened. Once aware of this, tunnels were opened cautiously so that the egg might always be recovered, but even then, an occasional burrow was found in which the crickets bore neither eggs nor any evidences of parasitization. Careful excavating led to the suspicion that possibly no eggs had been deposited on them, so a number of wasps were examined for eggs. The abdominal contents of 22 wasps were investigated before one was discovered emptied of eggs, yet this individual had just completed a two-cricket nest and closed it before being taken. The nest was opened with more than customary caution, but no eggs were found. Subsequently, another wasp taken in this condition, had caught and deposited the first cricket in her burrow before being collected. Whether these instances represent females exhausted of their eggs, or initially infertile, is a question, but the incidents are of interest in showing that there are apparently other stimuli in addition to the presence of eggs in the oviducts which prompt the wasp to begin her complicated activities.

Lack of Protection from Fly Egg Parasites.—On the occasion in which the first positive evidence of the parasitic activities of the flesh flies came to light, the author was watching a cricket wasp place her first victim in the nest. The tiny fly, very much in evidence as the wasp busied herself about the tunnel,

Fig. 7. Showing one of the two burrows in which four crickets were found. The tunnel has been cut away at the side to expose the insects. They are jammed against each other without the usual dirt bulwark separating them. The entrance to the nest lies just beyond the right edge of the photograph.

had followed the wasp from the point where the struggle with the cricket had taken place, back to the burrow. Here, the parasite waited until the wasp had flown away to find another victim before entering the tunnel. After a few minutes, believing she had emerged, the author pulled the cricket out with a pair of forceps to find, as she flew out, that the fly was still busy. The wasp egg was characteristically placed above the metacoxa, this time the left, and attached to this on the side and at the middle, was a wriggling mass which contained 14 fly larvae, already investigating the future food supply.

An occasional wasp packs a dirt wall upon the first cricket brought to the nest, but the majority leave the cricket entirely unprotected from the flesh flies. The number of grubs larviposited by the fly seems to vary from 12 to 20, and these are invariably placed on or near the wasp egg. They may or may not attack the egg, but usually immediately set about entering the cricket.

Number of Crickets Placed in the Nest.—In an average time of 12 minutes, 49 wasps returned with the second victim. This was placed in the burrow in front of the first cricket and, after depositing the egg, the wasp then set about closing the nest. As a general rule, only two crickets were placed in a burrow, but one and three were not uncommon, while the author twice found four packed tightly into solitary tunnels of more than average length and depth (Fig. 7). Cowan (1929) states that ". . . . it is reported that as many as five pupa cases have been taken from one burrow. . . ." Quite often, where wasps' nests were concentrated, the author found four and five crickets in what was apparently one burrow, but all of these resolved themselves into a juxtaposition of two or more separate nests, unwittingly dug by wasps in ground previously occupied.

E. Closing the Burrow

Method Employed.—A typical example of the specific behavior of the wasp during this phase is exemplified by an individual observed during the early morning hours. A few minutes after dragging the second cricket into her nest, she re-appeared at the surface and set about closing the nest. After scratching some loose dirt in, a large pebble was rolled in. Several times a dried, twisted serviceberry leaf *(Amelanchier alnifolia)* was pulled into the hole, then pulled out. Next she settled down to tamping in methodically the soft, excavated soil lying about the entrance of the nest. First she faced directly away from the entrance, and kicked dirt backwards beneath her with the forelegs, to the edge of the burrow. When the amount gathered there seemed satisfactory, she faced about and proceeded to tamp it in by the simple process of bunting it into the open hole with her mandibles, and packing it securely.

The amount of energy expended in tamping, and the amount of labor involved in carrying twigs, pebbles, etc., and in placing them, was always attested by the humming note of her wings. If the object she sought to incorporate into the tunnel was too heavy, she left it, as she did a twig three times her length and her own diameter through, which she could move only with difficulty. Few rocks were available, and twigs, leaves, and dirt had to suffice. Since she spent much time tugging at firmly-imbedded straws and

stalks, and packing tiny dirt fragments to fill in with, she was slower at the job than was usual in the locality.

Nine minutes later (8:45 a.m.) the wasp had the little mound above the closed entrance completed, and flew away. At 8:48 she returned for her first inspection, arranged a few sticks, and left. At 9:00 sharp she flew down again, and left permanently at 9:04 after packing a few more twigs and tidying up a bit.

The closure of each burrow was invariably terminated by the construction of a low, but definite, mound above the closed entrance. Generally, this mound was topped with a crude pavement of pebbles. Some wasps piled these pavement pebbles on more-or-less haphazardly, while others took pains to insert them carefully into the loose mound. In watching more than three score of these wasps during this phase, the author never saw any tamping use made of a pebble, as described by the Peckhams, but there were individuals who were not content to drop the pebble on the mound, but who were seen setting the stones firmly in the soil by moving it with their mandibles until its position seemed satisfactory.

Where pebbles were not available, the wasps placed twigs, sticks, and leaves on the mound. This phase of the nest-closing activities was gradually terminated by movements of an increasingly desultory nature. Finally, when the mound was conspicuously topped with pebbles or twigs, the wasps flew off, to return one or several times, usually within the ensuing ten minutes, to inspect the nest.

The humming of the wings was consistently heard outside the nest only during these closing activities.

F. Statistical Survey

The average number of nests dug by each wasp during the six days of maximum activity on the ridge is not known with certainty but, from estimates based on the length of time taken for a wasp to dig, stock, and close a burrow, the author believes that the average nest-building capacity approximates one and one-half burrows per day. On this basis, it becomes apparent, if the above estimate is reasonably accurate, that there were in the neighborhood of 30,000 wasps working in the mile by half-mile area. Comparison with the parasitization figures obtained below, brings to light the fact that the number of wasp larvae potentially destroyed (approximately 45,000) by the wasps' parasites, is one-third greater than the maximum total of wasps preying upon the cricket band. The significance of this will become more apparent in the discussion of parasitization below.

In *Quadrat D*, an acre of thinned and alkali-stunted sagebrush midway on the ridge, an average of six completed burrows per square yard was obtained at the end of the sixth day after the initial appearance of crickets and wasps. Since the average number of crickets deposited in a burrow is two, at least 58,000 crickets had been buried by the end of the sixth day. This figure is more consistently raised to the round number of 60,000 by considering (1) crickets paralyzed but abandoned when the wasp could not find her nest on

the return trip, (2) crickets left beside unclosed burrows whose owners had been killed by mice or shrews (see below), and (3) crickets in burrows opened and abandoned by the Red-banded wasp *(Stizoides unicinctus)* (see below). In all instances, these last had been parasitized by the flesh flies.

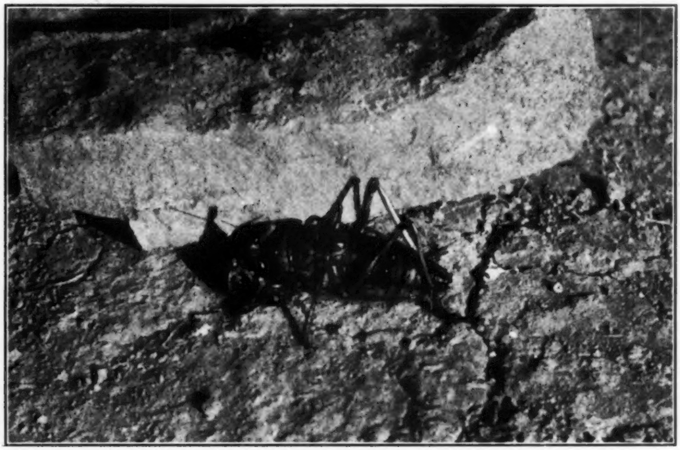

Fig. 8. An example of cannibalism common to the species. When found, this avid male had eaten and discarded all the victim except the thorax, which still bore two feebly-moving legs.

Half a Million Buried Crickets.—The data obtained for the remaining quadrats revealed the following figures: (1) *Quadrat A* contained an average of one-fifteenth of a completed burrow per square yard, which, for the enclosed 240 acres, totalled 77,424 burrows or 154,848 crickets; (2) *Quadrat B* contained an average of one-fifth of a completed burrow per square yard, which, for the enclosed 60 acres, totalled 58,080 burrows and 116,160 crickets; (3) *Quadrat C* contained an average of one burrow per square yard, which, for the enclosed 19 acres, totalled 91,960 burrows and 183,920 crickets; (4) *Quadrat D* contained 58,080 crickets. The combined paralyzed cricket population of the mile-by-half-mile area amounted to 513,008 crickets representing 256,504 burrows. This very probably underestimates the true figure by at least 50,000 crickets for the reasons enumerated in the preceding paragraph.

G. ENEMIES OF THE WASP

Parasites. (a. Flesh Flies).—Numerous factors restricted the efficiency of the black wasp as a control of the Mormon cricket. Three egg parasites and five predators of the wasp are known to the author, and all are significant checks upon the insect, materially reducing its numbers.

The small flesh flies *Euaraba tergata* and *Eumacronychia elita* were the most numerous of the wasps' parasites, and succeeded in infesting over 10%

or an estimated 6300 of the wasps' eggs and larvae in *Quadrat D.* To determine the probable percent of infection of the remaining quadrats, *Quadrat A* was sampled first, since this was expected to contain the least degree of parasitization. On this section, 350 burrows were opened before a parasitized cricket was found. Since time did not permit further sampling in this quadrat, this was taken as the unit number, and 350 burrows were opened in *Quadrats B* and *C*, respectively, in which the results were four and 30 parasitized burrows, respectively. On the basis of the sampling already done in *Quadrat D,* a parasitization of 366 burrows in the 350 square yards could be expected. These figures suggest that the number of burrows infected by the flesh flies would approximate 20,000 for the area studied.

(b. Red-banded Wasp).—A third egg parasite, the Red-banded bembicid wasp, *Stizoides unicinctus* (Say), which is somewhat smaller than the cricket wasp, digs up the closed burrow, destroys the egg by chewing it, and lays an egg of her own on the cricket, provided no flesh flies have preceded her. After re-closing the nest, the wasp flies to another burrow and repeats the performance. The first time the author noted this parasite was during an early morning vigil. While watching the small fly-catching bembicid *Stictiella pulla* (Handlirsch) tending her burrow in a sandy clearing, a Red-banded wasp flew rather clumsily into the clearing, and wandered about until chancing upon the pebble mound marking a newly-completed cricket wasp burrow. This was investigated laboriously, and then she began to dig into it. Her efforts at first seemed aimless, and the excavating, although strenuous, did not seem to be producing results. Finally, however, the wasp began working steadily, and soon disappeared from sight. She remained in the tunnel for longer intervals as she worked her way deeper into the nest. At first, when working in the entrance, the wasp periodically flew up into the branches of an adjacent sagebrush, perhaps to cool off and rest, but as the work progressed, she only emerged at long intervals to remove the excess dirt accumulating in the burrow. Two small flesh flies flew persistently about the hole, one flying in several times beside the working wasp.

At 10:15 a.m. (55 minutes after the wasp's first appearance), she emerged from the hole. The first hint that she was coming out was a miniature landslide into the enlarged entrance. Then her head and thorax came into view, and she could be seen throwing dirt backwards into the tunnel. Emerging, she scraped a little more detritus into the burrow, obliterating the tunnel, but leaving a conspicuous pit in the ground, and after flying about the clearing, wandered off with apparent aimlessness.

Returning to the site at 1:30 p.m., the author found the nest still closed; upon opening it, the long-dead remains of a cricket wasp were discovered beneath the loose soil of the entrance. At the end of the tunnel lay a paralyzed, but still living male cricket, placed within the burrow sometime during the early morning hours of the same day. No cricket wasp egg was to be found, nor any traces of one, but a hole above the left metacoxa plainly showed where something had gained entry. Cemented loosely over the wound was a ball of mud, formed by escaping secretions. Macroscopic dissection of the cricket, which had passed beyond the ability to squeak, showed the abdominal cavity

adjacent to the wound to contain some dozen tiny, wriggling flesh fly larvae, and more were undoubtedly scattered through the soft tissues of internal organs.

Further investigations of the parasitic Red-banded wasp's activities revealed the following characteristics of behavior:

(1) The wasp was an untidy worker, never leaving a burrow as she had found it, but always terminating her labor when she had barely re-filled the hole, thus leaving a diagnostic pit in the ground; (2) She never failed to chew the cricket wasp's egg thoroughly when she invaded a burrow; and (3) she never laid an egg of her own upon the cricket if the latter showed any evidences of flesh fly parasitization. How she always knew was a mystery, for in some of the nests she opened, the fly larvae had already pierced the abdominal wall of the cricket and migrated to the interior without disturbing the cricket wasp egg on the outside.

A survey of *Quadrat D* revealed a 7.5% parasitization by this wasp, raising the total of potentially destroyed cricket wasps to over 10,000 for this quadrat alone. Sampling (see preceding discussion of flesh fly parasitization) failed to reveal any trace of *Stizoides unicinctus* infection in *Quadrat A*, but three cases were discovered in *Quadrat B*, and 27 in *Quadrat C*. This close correspondence between experimental results and theoretical expectations derived from the flesh fly data, tends to make the author confident that, inadequate as the sampling was, the results obtained were probably indicative of the true state of affairs.

Predators. (a. Mammals).—Equally important in restricting the wasps' beneficial work are the insects' predators. The Sierra shrew (*Sorex vagrans amoenus* Merriam) and the short-tailed Grasshopper mouse (*Onychomys leucogaster brevicaudus* Merriam) attacked and fed on the adult wasps in the early dawn hours when the latter were working on their nests. A survey within *Quadrat D* showed that predation amounted to one wasp per 15 square yards, or approximately 10%. This figure is undoubtedly an underestimate, since it is based entirely upon the number of uncompleted burrows which could be correlated with the abundant wasp remains; there is little doubt that wasps were killed who had not yet begun to build burrows, and so left no record of their death. From strong circumstantial evidence, the author is inclined to attribute approximately 90 to 95% of this destruction to these two mammals, the remaining 5 to 10% constituting approximately the observed amount of predation by birds.

The attacked wasps were found decapitated and eviscerated, the tip of the abdomen—with its sting—being nipped off and the contents pulled out, leaving the cavity emptied of all but a few muscle fragments. In addition, the majority of victims had large areas of the thoracic musculature eaten into. When the mammalian depredations were at a maximum, an early morning visit to *Quadrat D* found the ground at certain points well scattered with dead and dying wasps. One decapitated and eviscerated wasp found at daylight—from its condition, but a short time after the attack—lived for four hours before the last feeble leg movements ceased. When first noticed, it was gyrating

wildly about the clearing on its back, being unable to co-ordinate walking movements.

No data are available concerning the relative roles of the grasshopper mouse and the shrew in this wasp destruction, but trapping showed both to be abundant on the ridge, especially in the denser serviceberry—sagebrush associations. Both wasps and crickets were used as bait, and were readily taken. The Sonoran White-footed mouse (*Peromyscus maniculatus sonoriensis* Le Conte) was also taken, but the presence of this normally herbivorous rodent cannot be regarded as significant, although the great predominance of the competing Mormon cricket may have somewhat altered the mouse's diet.

In these areas of maximum mammalian attack, unattended and paralyzed crickets were commonly found on the ground, but these were practically always eaten by healthy crickets before they could recover. However, the crickets found the attacked wasp hulks largely unpalatable, and disturbed few of them.

(b. Birds).—The number of birds seen to capture the cricket wasp was surprisingly small compared with the variety that fed upon the cricket (La Rivers 1941). Only five species were observed to take the wasp as food, and the activities of only three of these could be considered of any moment in reducing the numbers of the wasp. These, in order of their importance, were the Sage thrasher (*Oreoscoptes montanus* (Townsend)), the Brewer blackbird (*Euphagus cyanocephalus* (Wagler)), and the Sparrow falcon (*Falco sparverius* Linné). The White-rumped shrike (*Lanius ludovicianus excubitorides* (Swainson)) and the Desert hornedlark (*Otocoris alpestris leucolaema* (Coues)) completed the list.

The Sage thrasher was most active in the early morning hours when the wasps were busiest. It was one of the commonest sagebrush birds, but its dull colored plumage and shyness kept it inconspicuous, while the less numerous but more boisterous Brewer blackbird seemed at first sight to be more prevalent.

As in the case of the mammals, the wasps were decapitated and eviscerated, but only the digestive and reproductive tracts were eaten. However, the author is of the opinion that these birds could not alone be considered significant checks upon the cricket wasp, but would only become important when parasites and other predators had reduced the wasp numbers to a point where any additional predation, no matter how slight, exceeded the critical point. Birds found the crickets more palatable and more easily taken than the wasps and their attacks upon the latter must be rare in regions of normal wasp concentration.

The Cricket as a Possible Predator.—Before fully realizing the all important role played by these predators, the author was inclined to fix the cricket with some of the blame for this destruction. While largely relinquishing this supposition, there still remained some evidence that they may eat wasps under certain circumstances, for an occasional cricket was found feeding on wasp remains that the author could not be sure were merely chanced upon after being left by a mammal or bird. Further corroboration of this suspicion came from the following incident. At 7:35 a.m., while watching the industry of a

ground wasp (*Dasymutilla ursula* (Cresson)), the author's attention was attracted to a cricket pursuing an object at a fast walk. The object proved to be a wasp intent on closing her nest. She paid no attention to the cricket, merely moving quickly on as he came up to her. His was apparently the singleness of purpose of an empty stomach. Four times the cricket caught up with the wasp, and laid his protarsi on her, and four times she eluded him and went unconcernedly on. At no time did the cricket show the usual fear of the wasp, and at no time did the latter become belligerent. The last time she was annoyed, the wasp flew away, and the cricket wandered off.

The author has found that wasps who were engaged in other phases of their activities than that of cricket hunting were not inclined to use the sting in self defense. A working wasp could be picked up in the fingers without danger, if the capture was accomplished gently, and without undue pinching. She was invariably greatly annoyed, and struggled and hummed vigorously, but made no other attempt to defend herself than to try and bite. Not once did the sting appear. If the unorthodox cricket mentioned above had been successful in getting hold of the wasp, it is conceivable that his greatly superior jaws would have made short work of her.

Summary

The black cricket wasp, *Chlorion laeviventris*, is undoubtedly the most important parasite of the adult Mormon cricket *(Anabrus simplex)*.

The wasp overcomes the cricket by mounting its back and stinging it between the legs, which nearly always results in a temporary paralysis, and sometimes in death. The victim is then dragged to a burrow, which is always, in the author's experience, dug before the cricket is attacked, but which may, from the observations of others, be dug afterward. In the burrow, an egg is attached to the cricket's body just above the insertion of one of the hind legs, and the cricket tamped in with dirt. Two crickets are generally placed in one burrow, but one and three are often found, while four individuals in the same burrow is rare, although five have been supposedly reported from one burrow. Each burrow is completely re-covered, and topped with a characteristic pile of pebbles, or sticks and bits of earth.

In the area studied, a rectangle one mile long by one-half mile wide, a total of somewhat over 500,000 buried crickets was reliably estimated from 1182 counting stations. At an estimated rate of one and one-half burrows per day dug by each wasp, the number of wasps active in the area can be tentatively placed at 30,000.

The efficiency of the cricket wasp as a control of the cricket is seriously counteracted by three wasp egg parasites, and five major predators of the adult wasp. Of the egg parasites, the two sarcophagid flesh flies *Euarba tergata* and *Eumacronychia elita* are the most significant, destroying an estimated total of nearly 30,000 wasp eggs and larvae, while the Red-banded bembicid wasp *(Stizoides unicinctus)* is nearly as destructive. being responsible for the loss

of approximately 15,000 wasp eggs and larvae. These figures, while necessarily approximate estimates, nevertheless show the trend of the factors involved.

Of the five important predators of the adult wasps, two mammals, the Sierra shrew *(Sorex vagrans amoenus)* and the Short-tailed Grasshopper mouse *(Onychomys leucogaster brevicaudus)* are the most significant, the depredations of these two species accounting for from 90 to 95% of the total adult wasp destruction, while the remaining predators, three species of birds *(Oreoscoptes montanus, Euphagus cyanocephalus,* and *Falco sparverius)* destroyed the remainder.

There is also a strong possibility that crickets may occasionally catch and eat adult wasps.

Conclusions

It is a well-known fact that insect parasites of hosts with rhythmic life cycles necessarily exhibit corresponding rhythms in their own cycles. In the case of the Mormon cricket—Cricket wasp relationship, available evidence indicates that a period of from four to eight or more years may elapse between the time that the crickets indigenous to any one area break out in epidemic proportions and the time that the wasps themselves reach equilibrium with them.

However, although it may take several years to reach equilibrium, the beneficial wasp population may be reduced to insignificance in the course of one season if the crickets upon which they prey are suddenly reduced in numbers. This has happened repeatedly in the history of the animals. Seasonal vagaries, such as drought, extreme cold, prolonged snows, or a mild winter followed by a severe spring, may entirely decimate cricket bands over widespread areas, with the attendant loss of parasites from lack of suitable hosts. The natural reservoir of wasps is maintained by the few crickets still extant in the area, and by grasshoppers and various caterpillars upon which the black wasp also preys, but a noticeable increase in wasp numbers does not take place until several seasons after a similar increase in cricket numbers occurs. Attempts to effect this by keeping artificially-reared wasps on hand at all times could not aid in remedying the situation, unless great numbers were available, for the wasps are comparatively slow in reaching parity with their hosts. The artificial introduction of wasps into areas where crickets are epidemic and wasps few would still mean the lapse of several years before any type of equilibrium began to be maintained, although such action would be important in ultimately checking the pests.

The most favorable developments of this type will probably have to await a thorough investigation into the life history of another of the parasites of the Mormon cricket, the tiny scelionid wasp *Sparaison pilosum* Ashmead, which is probably the most important of the crickets' natural controls, since it attacks the eggs of the insect, and has been reported in several instances as practically eliminating the cricket hatch in previously heavily-infested localities.

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Contributions to the Osteology of the Post-cranial Skeleton of the Amphisbaenidae

Rainer Zangerl

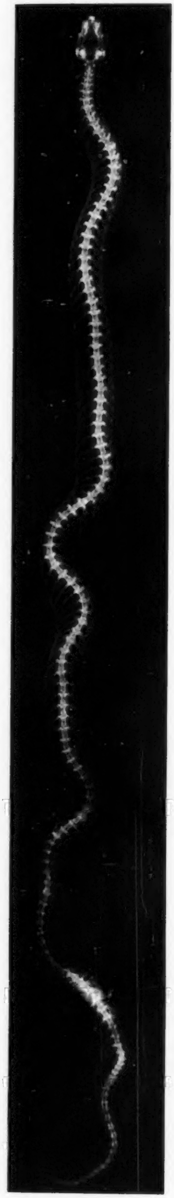
1. Introduction

The post-cranial skeleton, unlike the skull of the Amphisbaenidae (Zangerl, 1944), does not exhibit as many characters peculiar to this group of reptiles. In some respects there are similarities with the post-cranial skeleton of the snakes, (e.g., the large number of presacral vertebrae; distally forked ribs in the sacral region; no haemapophyses, but paired ventral processes in the tail region, analogous to haemapophyses), in other respects with that of the lizards (e.g., the structure of the vertebrae lacking zygosphen-zyganthrum connection; the presence of a shoulder girdle and front limbs in the genus *Bipes*, with a lacertiloid carpus, but a strange phalangeal formula of 3, 3, 3, 3, 3; vestiges[1] of a shoulder girdle in *Blanus cinereus*, and other forms). Furthermore there are similarities which the amphisbaenids have in common with the snakes and the limbless forms among the lizards (e.g., lymphapophyses in the sacral region). Practically all of these characters are clearly adaptive and do not suggest a close relationship to either the lizards or the snakes. Scattered information concerning the post-cranial skeleton of the Amphisbaenidae can be found in the literature. Most descriptions and illustrations concern girdle and limb vestiges (Joh. Müller, 1832; Dumeril and Bibron, 1839, 1854; Gervais, 1853; Fürbringer, 1870, 1900; Smalian, 1885; Cope, 1892a; K. H. M. Müller, 1900) and need to be revised and expanded.

The present report is based on the same specimens which furnished the material for the descriptions of the skulls. I wish to express my very best thanks to Dr. Thomas Barbour and Mr. Arthur Loveridge for the privilege of studying these specimens. Dr. K. P. Schmidt of the Chicago Natural History Museum kindly supplemented the material with the loan of a specimen of *Blanus cinereus* from Spain, and part of a specimen of *Diplometopon zarudnyi* from Saudi Arabia, and Dr. Charles M. Bogert of the American Museum of Natural History with an example of *Anopsibaena kingii* from Cordoba, Argentina. Dr. Hobart Smith kindly contributed an excellent x-ray plate of *Bipes canaliculatus* which is here reproduced (Fig. 3) and the species is included in the descriptive part. The specimens were cleared and the bones and calcified cartilages stained with Alizarin Sulfonate of Sodium according to a modified Spalteholz technique described elsewhere.[2]

[1] Such terms as "reduction," "vestige," "remain," etc., commonly found in morphological accounts, are used in a purely comparative sense and carry no phylogenetic implication.

[2] Schinz, H. R. and Rainer Zangerl. 1937—Beiträge zur Osteogenese des Knochensystems beim Haushuhn, bei der Haustaube und beim Haubensteissfuss. Denkschriften Schweiz. Naturforsch. Ges. **72**(2).



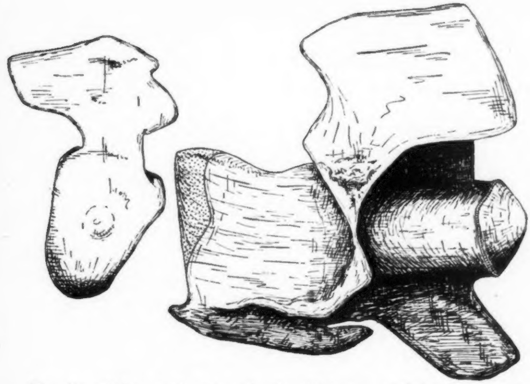


Fig. 1. Atlas and axis of *Amphisbaena fuliginosa* in side view. About 20 times nat. size.

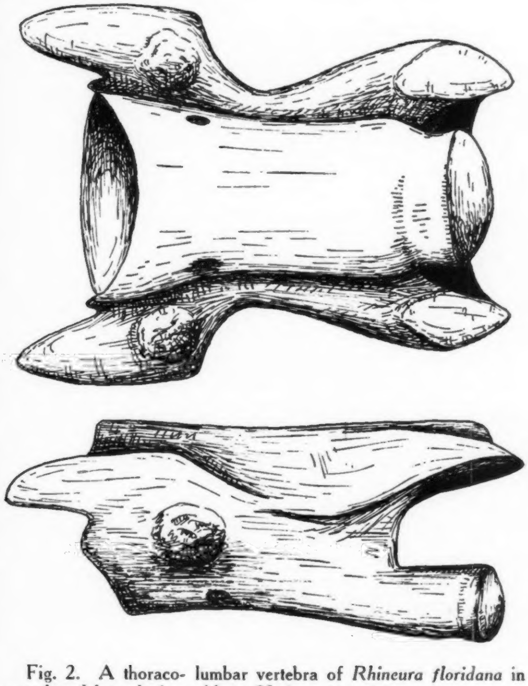


Fig. 2. A thoraco- lumbar vertebra of *Rhineura floridana* in ventral and lateral view. About 25 times nat. size.

Fig. 3 (left). X-ray photograph of *Bipes canaliculatus*. Slightly less than nat. size.

2. General Morphology of the Post-cranial Skeleton of the Amphisbaenidae

The post-cranial skeleton of the Amphisbaenidae consists of a long vertebral column, the number of vertebrae, procoelous throughout, ranging from 85 (in *Trogonophis*) to 155-156 (in *Rhineura*) among the examples herein studied. All the vertebrae, except the first few and those of the tail, are equipped with freely movable ribs. Vestigial sternum and shoulder girdle elements are probably present in all genera. These structures are best developed in *Bipes* which has, in addition, well developed front limbs. The pelves and hind limbs are highly vestigial in all of the forms under observation.

a. THE VERTEBRAL COLUMN

On the basis of the adult skeleton, four regions of the vertebral column can be distinguished for the purpose of description. These are chiefly characterized by the presence or absence of freely movable ribs and typical transverse processes.[3]

A very few vertebrae at the anterior end of the column possess no ribs; these shall be called cervical vertebrae. The cervical region includes the atlas, axis and 1 to 2 vertebrae behind the axis. The thoraco-lumbar region includes all the vertebrae which carry freely movable, simple ribs. The vertebral centra in the anterior part of this region are shorter than those further back, the transition being gradual.

In the general neighborhood of the cloaca, where the vestiges of the pelvis and the hind limbs are located, the axis skeleton exhibits a few interesting features. Usually one pair of free ribs (at the end of the thoraco-lumbar series) is distally forked as in snakes (Salle 1881).[4] The following 2 to 4 vertebrae have deeply forked transverse processes. Some of these vertebrae with distally forked ribs or deeply forked transverse processes obviously represent sacral vertebrae, but for want of a synostotic connection between the pelvis and the axis skeleton, it is not possible to designate any of these vertebrae as sacrals, nor to ascertain their probable number. This region shall here be called cloacal region. The tail region is always very short in amphisbaenids. The vertebrae have straight transverse processes and relatively large, paired, ventral processes.

The atlas is simple, usually consisting of two dorsal arch pieces which may be aspinous and dorsally separate, as in *Sphenodon* or form an indication of a dorsal spine. Frequently there is a ventral cross bar, lying immediately in front of the odontoid process, most probably representing the hypocentrum (intercentrum) of the atlas. The latter bone is seen in various stages of reduction. A proatlas was not observed. The axis is somewhat larger than the adjoining vertebrae. The odontoid process (dens epistrophei) is very well developed, in fact as big as the centrum of the axis proper and often wider than the latter. The shape of the odontoid process is shown in Fig. 1. The dorsal and ventral

3 The general term "transverse process" is here used for all lateral processes of the vertebrae, since the neuro-central suture could not be observed and the presence of pleurapophyses can only be detected in embryonic or very young specimens.

4 In some snakes there are several pairs of such ribs in the region of the cloaca.

surfaces of the process are flattened. The surface with which the atlas articulates stands vertical and extends from the front of the process backward on both sides almost to the body of the axis proper. It appears safe to conclude that the shape of the odontoid process excludes the possibility of rotation of the atlas (slight rotation at this point is possible in *Sphenodon* and *Iguana,* according to Evans, 1939) but provides, instead, wide lateral movements of the head. The remaining neck vertebrae (where present) resemble those of the thoraco-lumbar region except for the lack of transverse processes. The axis as well as a variable number of adjoining vertebrae may possess low hypapophyseal keels.

The vertebrae of the thoraco-lumbar region (Fig. 2) are quite uniform in appearance. Those of the anterior third of this region are somewhat shorter than those further back. The procoelous vertebral centrum is wider at its concave end than near its posterior end, where there is often a marked lateral constriction. To either side of the centrum and in the anterior half of it, there are openings which lead to the interior of the vertebral body. Sometimes these foramina are rather large and conspicuous. The low, but wide neurapophysis possesses strong zygapophyses. Immediately below the prezygapophyses originate the short, knobby transverse processes. The glenoidal surfaces of the prezygapapophyses face upward and slightly inward, those of the postzygapophyses downward and somewhat outward. The ribs in the thoraco-lumbar region are single-headed and are in no way connected with the sternum. Often there are small bony processes next to the capitula of the ribs facing caudad, or rarely craniad (*Rhineura*) to which tendons of epaxial muscle segments are attached.

The vertebrae of the cloacal region are of about the same size as those of the foremost portion of the thoraco-lumbar region. The neurapophyses are somewhat higher than elsewhere and often roof-shaped. The transverse processes of the first cloacal vertebra are short and their articulation surfaces are concave. Attached to these processes are strange ribs which are most often distally forked, as in the anterior part of the cloacal region in snakes (Salle 1881). The transverse processes of the following vertebrae carry no ribs; they are relatively long and forked at their places of origin. Between the diverging limbs of each fork there are, according to Salle 1881, lymph-hearts as in the corresponding region of the vertebral column of snakes and limbless lizards. Some of the cloacal vertebrae (usually only the posterior ones) possess paired, ventral processes (functional equivalents of haemapophyses) which are short at first and increase in size toward the tail region.

The caudal vertebrae decrease in size but slightly towards the end. Well developed neurapophyses are found to the very tip of the tail. The transverse processes are moderate in length, straight, and sometimes faintly forked distally. The ventral, paired "haemapophyseal" processes are rather large and the pairs often fuse ventrally. The last few vertebrae of the tail tend to fuse with one another.

The numerically varying position of the cloacal region in different amphisbaenids and the variable qualitative and quantitative development of the ribs,

transverse and ventral processes at the end of the cloacal series (accompanied by occasional irregularities) suggest a phylogenetic displacement of this region towards the tail, a process that did not proceed at equal speed in the different species and seems to have not yet come to a standstill.[5]

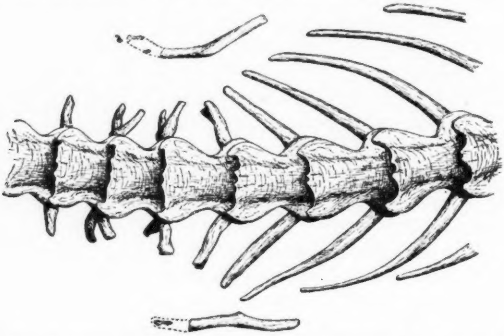


Fig. 4. Cloacal region and pelvic vestiges of *Rhineura floridana* in dorsal view. About 7 times nat. size.

b. THE STERNUM AND SHOULDER GIRDLE[6]

1. *Bipes biporus.*—These structures have been described and figured repeatedly by earlier students(Joh. Müller, 1832; Dumeril and Bibron, 1854; Fürbringer, 1870; Cope, 1892), but the familiar technique of dissection and maceration, available to these authors, was unsatisfactory for the study of such delicate elements. Important features of the shoulder girdle were overlooked and no attempt was made to investigate the autopodium.

The sternum (Fig. 5) consists of a somewhat quadrangular piece of calcified cartilage (probably paired in origin) and a long, slender, calcified-cartilaginous xiphoid process. Cope (1892) correctly illustrates the sternum except for the fact that he represents all but the most posterior part of the xiphoid process as bony in nature.

5 For further information concerning the writer's views on regional variation of the vertebral column, see Schinz and Zangerl (1937, pp. 126-129), Abh. Schweiz. Naturforsch. Ges. **72**(2); also Zangerl (1935), Abh. Schweiz. Pal. Ges. **56**, pp. 55-64; furthermore see Mettig (1939), Anat. Anz. **88**, pp. 1-48. The genetics of regional variation of the vertebral column was worked out by Kühne (1936), Zschr. f. Morph. u. Anthropol. **35**.

6 Although there are statements and illustrations in the literature of cartilaginous or bony vestiges of the sternum and shoulder girdle of various amphisbaenids (Fürbringer, 1870: *A. fuliginosa;* Smalian, 1885: *Amphisbaena fuliginosa* and *Trogonophis wiegmanni;* Fürbringer, 1900: *A. alba, A. fuliginosa, Blanus cinereus, B. strauchi, Trogonophis wiegmanni;* K. H. M. Müller, 1900: *Blanus cinereus, B. strauchi, A. fuliginosa, Cephalopeltis scutigera, Trogonophis wiegmanni*), no such elements could be found in the forms herein studied, except in the genera *Anobsibaena, Blanus* and *Bipes.* This may partially be due to the technique used (uncalcified cartilage is but rarely visible) and probably also because some specimens were skinned before they were cleared and stained. Subsequent clearing of an additional specimen of *A. fuliginosa* did not reveal any sternal or shoulder girdle elements.

The shoulder girdle (Fig. 6) consists of three elements. One relatively large bone is medially attached to the quadrangular portion of the sternum. It is a flat plate, narrow in the middle and wide at both ends. Its longitudinal axis forms an angle of about 90° with that of the animal. It resembles somewhat the fused scapulo-precoracoid of *Sphenodon*. The pre-coracoid part of the element is pierced by a foramen, presumably for the passage of the supracoracoid nerve. The glenoidal cavity is saddle-shaped and located at the posterior edge, partly on the ventral surface of the bone and close to its medial border. A calcified cartilage element, commonly referred to as suprascapula (figured as a bony element by Cope, 1892) is fastened to the lateral edge of the scapulo-precoracoid as in lizards and in *Sphenodon*.

In front of the scapulo-precoracoid lies a minute, bony bar, unattached to any other part of the shoulder girdle or the sternum (Fig. 6) which was overlooked by the previous workers. According to its position it represents a vestigial clavicle.

2. *Blanus cinereus*.—As far as this writer can see, Fürbringer (1900) and Max Müller (1900) mention and figure the shoulder of *Blanus cinereus* and *B. strauchi*. Both authors figure vestiges of the sternum as well as the girdle, but their figures differ in many ways and all of them differ from the one given in this report (Fig. 7). This is perhaps due to individual variation, rather than faulty observation. In the cleared and uninjured specimen (C.N.H.M. No. 603) there is a surprisingly well developed shoulder girdle on the right side of the specimen, but its left counterpart is absent (Fig. 7).

The sternum consists of a few irregular patches of calcified cartilage undoubtedly embedded in a larger uncalcified piece, the extent of which could not be made out. Aside from the shape and size of the different shoulder girdle elements, the latter resemble very much those of *Bipes biporus*. The clavicle, however, is much larger compared to the scapulo-precoracoid than in *Bipes biporus* (Fig. 7).

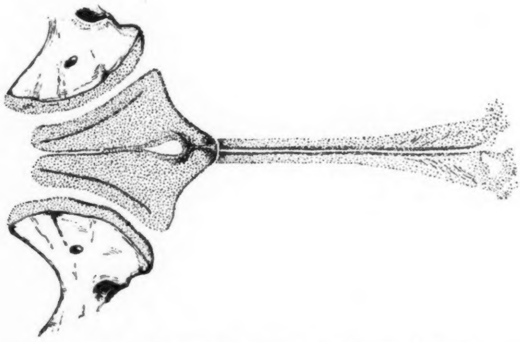


Fig. 5. Sternum and adjoining shoulder girlde elements of *Bipes biporus*. Dotted areas indicate calcified cartilage. About 12 times nat. size.

c. THE FRONT LIMBS

The front limbs of *Bipes* are short, but fully developed in every way but in size. The humerus is a fairly straight bone, slender in the middle and greatly expanded at both ends. Only a small portion of the proximal end serves as caput humeri; the tubercula majus and minus are very large. The distal end of the humerus forms a simple trochlea. Above the elbow joint, riding on the trochlea humeri there is a tendon ossification (patella ulnae), located in the tendon of the M. triceps brachii. The radius and the ulna are of about equal length. Both are fairly straight bones, only moderately enlarged at both ends which consist of calcified cartilage. The radius is slightly smaller in diameter than the ulna. A spatium interosseum is present, since the radius and the ulna diverge distad.

The autopodium has not been described or figured previously. The carpus consists of 8 ossified elements; in addition to these there are an os pisiforme

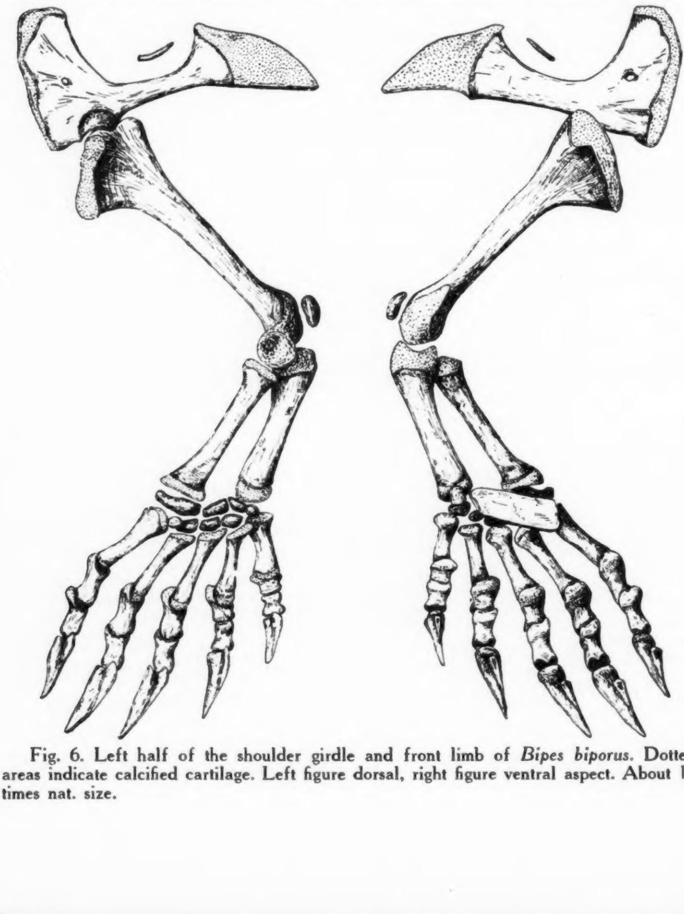


Fig. 6. Left half of the shoulder girdle and front limb of *Bipes biporus*. Dotted areas indicate calcified cartilage. Left figure dorsal, right figure ventral aspect. About 12 times nat. size.

and a large, thin sesamoid plate on the ventral side of the carpus proper (Fig. 6). The flexor tendons of the digits all convert towards this plate and are fastened to it. The interpretation of the 8 carpal bones offers little difficulty since they can well be compared with those of most lizards with well developed front limbs. The carpals are arranged in two transversal rows. In the proximal row are four bones, one immediately distal to the radius, a radiale, one distal to the ulna, an ulnare, and a third element, closing the spatium interosseum is here interpreted as a centrale in accordance with the morphology of the carpus of lizards (Born, 1876). The os pisiforme lies ventral to the distal tip of the ulna (Fig. 6). The remaining five carpals, carpalia distalia I–V, lie proximal to their corresponding metacarpals as in the lizard carpus.

There are 5 metacarpalia; Mc II and III are slightly longer than Mc I and IV; Mc V is the shortest. All metacarpals are moderately enlarged at their proximal ends.

The phalangeal formula is 3, 3, 3, 3, 3. In *Bipes canaliculatus* the number of phalanges of the 5th ray is likely to be less than 3 (see page 775). With the exception of the terminal ones the plalanges are short and strong. At their proximal ends they possess ventral cup-shaped projections which articulate with the distal joint surfaces of the more proximal elements and allow the bending of the digits only within limits. The endphalanges, wearing large, horny claws, are sharply pointed and each possesses two longitudinal ridges, one on the dorsal side which reaches beyond the proximal end of the element and probably serves as place of insertion for the extensor tendon and one on the ventral surface which forms a knob for the insertion of the flexor tendon (Fig. 6).

The front limbs of *Bipes* are of considerable general interest. They are very small compared to the size of the animal, but they are in no way vestigial. The shoulder girdle on the other hand seems to have undergone some reduction, since the clavicle in its present development hardly represents a primitive condition. Apparently, in *Bipes,* a process of reduction has begun in the region of the shoulder girdle without affecting the extremities at all. In *Blanus cinereus* the exact opposite is the case, there is a rather fully developed shoulder girdle, but no traces of the limbs; also, in the rear extremity of all amphisbaenids, the distal part of the appendicular skeleton has undergone the greatest degree of reduction.

The phalangeal formula of the hand of *Bipes* is strange. The number of phalanges of the first digit is larger, that of the second, third and fourth digits is smaller compared to the primitive formula of 2, 3, 4, 5, 3. To my knowledge no lizard has three phalanges on the first finger, in fact, higher phalangeal numbers are found only in a few groups of tetrapods which have reached a very high degree of aquatic specialization, e.g., in Ichthyosauria, Mosasauria, Plesiosauria, and some (distinctly aquatic) Nothosauria (e.g. *Lariosaurus balsami,* Cur.[7]).

One is tempted to dismiss the problem with the assumption that the polyphalangy of the first digit in *Bipes* developed in connection with its func-

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7 See Peyer, B. 1933-34—Abh. Schweiz. Pal. Ges. **53** and **54**.

tion as a digging device. In forms that use their hands for digging, it is very rarely the thumb which is greatly enlarged (e.g., in *Amyda*, in which the front limbs are used for swimming as well as for digging) and in none of these cases is the increase in size accompanied by polyphalangy.

d. THE PELVIS AND THE POSTERIOR LIMB VESTIGES

Remains of the pelvis are probably present in all amphisbaenids.[8] In *Bipes* and *Blanus* there are some additional vestiges of the rear limbs (Figs. 8 and 9). In all forms there is one bony bar which lies lateral and slightly ventral to the cloacal region of the vertebral column. It is about circular in cross-section and either straight or somewhat curved. In *Blanus* its ventral end is considerably enlarged. Connections between this bone and the vertebral column could not be found. This element is considered as the ilium to which other pelvic

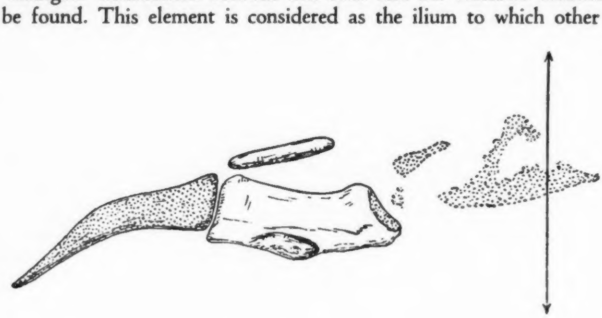

Fig. 7. Right half of shoulder girdle of *Blanus cinereus* in ventral view. Arrow indicates sagittal plane. About 30 times nat. size.

components might be fused. *Blanus* is the only genus in which a second element of the pelvis is present in the form of a small calcified cartilage platelet which lies near the ventral end of the ilium; it might be regarded as a pubis. In *Bipes* there are two bones and a calcified cartilage element besides the ilium. The latter possesses near its lower end a shallow joint cavity to which the second largest bone, the femur, is attached. The femur is short, flat and wider distally than proximally. Connected to its distal end are a minute, subtriangular bone and a bigger piece of calcified cartilage (Fig. 8). In *Blanus* the limb vestiges are represented by a femur only; it is circular in cross-section, and somewhat pointed distally (Fig. 9).

These structures bear a good deal of similarity with the pelvic and rear extremity vestiges of *Ophisaurus ventralis* (of which a cleared specimen is at hand for comparison) and with those of the Sirenia (except *Manatus latiros-*

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8 In *A. cubana, Trogonophis wiegmanni*, and *Geocalamus acutus* no pelvic vestiges could be observed. This is hardly due to the lack of such vestiges in these forms, but rather the result of an oversight when the specimens were skinned prior to being cleared and stained. The writer had the same experience with two specimens of *A. fuliginosa* but subsequent clearing of additional, unskinned specimens revealed vestiges as well developed as those of *Rhineura* or *Monopeltis*.

tris) and the wales. In *Ophisaurus ventralis* and *Halicore dugong* the pelvic vestiges consist of slender bones that are ventrally flat and wide. In both forms there is a clear suture either at mid-length (in *Halicore*) or in the ventral third as in *Ophisaurus*. In the latter form a tiny bone (not cartilage, as indicated by Cope, 1892) originates from the region of the suture. In *Bipes* there is no suture, but near the lower end of the pelvic bone there is a shallow acetabular cavity as in the oligocene sea cow *Halitherium schinzi*, Kaup. In view of the general similarity of position of the acetabulum, it would be reasonably convincing to assume that the pelvic elements of the amphisbaenids (e.g., in *Bipes*) also represent products of fusion of at least two pelvic bones. In *Blanus*, however, the pelvis is more primitive and represented by two distinct elements, probably a bony ilium and a ventral, calcified cartilaginous pubis. This situation suggests that in most amphisbaenids the two ventral elements (the ischium and the pubis) are absent, rather than fused to the ilium, in which case the acetabulum appears displaced. The interpretation of the zeugopodial elements in *Bipes* offers some difficulty, since the femur is obviously not in its original position to the pelvis and its surfaces do not give any clues as to its orientation. It seems reasonable, however, to assume that the limbs, once reduced to mere vestiges, were held close to the body and facing it with their ventral surfaces. If this assumption is correct, the tiny bone of the zeugopodium would represent the tibia.

3. Description of the Various Forms

a. AMPHISBAENA FULIGINOSA Linnaeus

The total number of vertebrae, including the atlas, of this species is 137. These are distributed over the previously defined regions of the vertebral column as follows: cervical region 3, thoracic region 103, cloacal region 2, caudal region 29. Atlas and axis are illustrated in Fig. 1. The atlas consists of only 2 arch pieces. The axis possesses a very large odontoid process which is ventrally keeled by a low, but long hypapophysis. The latter is followed by a second one originating from the centrum of the axis proper. The anterior, upper portion of the odontoid process apparently remains cartilaginous. The neurapophysis is laterally connected to the centrum and the odontoid process by a prominent crest which forms a tuberosity at its upper end, probably for the attachment of muscles (Fig. 1). The first vertebra of the thoraco-lumbar series possesses a pair of very minute ribs. The first 4 vertebrae in this region have hypapophyseal processes; these projections decrease in size from the first to the last. The tendon processes of the ribs are well developed and point caudo-dorsad. None of the cloacal vertebrae possess forked ribs. There are 2 vertebrae with forked transverse processes, however, both have "haemapophyseal" stumps. The latter continue with increase in size to the 2nd caudal vertebra where they fuse ventrally. In this species the last thoraco-lumbar vertebra also carries "haemapophyseal" ossifications. These are, however, not merely processes from the postero-lateral corners of the vertebral centra, but separate ossifications. Since they lie within strong tendons, it is possible that they represent tendon ossifications. The transverse processes of the tail vertebrae are very short.

The vestiges of the pelvis are confined to relatively large v-shaped bars, distally capped by partially calcified cartilage (Fig. 9).

b. AMPHISBAENA EWERBECKI Werner

An accurate count of the number of vertebrae of the vertebral column or its regions is not possible because the heads were cut off well behind the occipital condyles in both available specimens. The cloacal region consists of two or three vertebrae, none of which possesses forked ribs. "Haemapophyseal" stumps are present on the last thoraco-lumbar vertebra and on the cloacal vertebrae. In the tail region they are relatively long, and the pairs are, as in *A. cubana,* nowhere ventrally fused together, although the specimens are adult beyond doubt.

The pelvic vestiges are tiny, almost straight bars, slightly thicker at the dorsal than at the ventral ends (Fig. 9).

c. AMPHISBAENA CUBANA Peters

The vertebral column of this form consists of 120 vertebrae; 3 belong to the neck region, 100 to the thoraco-lumbar portion, 3 to the cloacal region and 14 to the tail. The atlas consists of neurapophyseal pieces only. These are longer dorsally than in *A. fuliginosa.* The axis is relatively smaller than in *A. fuliginosa,* has only inconspicuous hypapophyses, and no prominent lateral crests. The last neck vertebra and the first 2 of the thoracic region possess hypapophyses of about equal size. The tendon processes of the ribs are similar to those of *A. fuliginosa.* The first cloacal vertebra carries a pair of forked ribs, the remaining two cloacal vertebrae have normally forked ribs, and "haemapophyseal" processes. The latter are quite long in the tail, but are nowhere fused ventrally; this is perhaps due to the immaturity of the specimen.

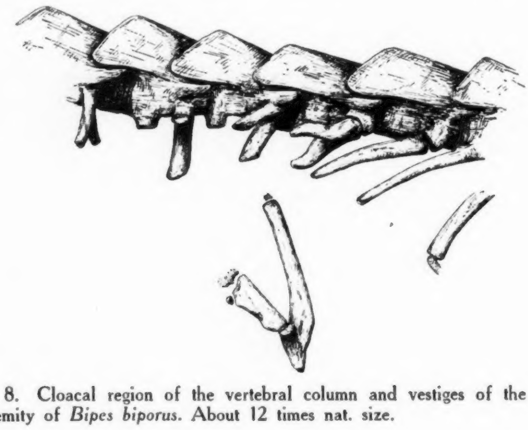

Fig. 8. Cloacal region of the vertebral column and vestiges of the pelvis and rear extremity of *Bipes biporus.* About 12 times nat. size.

d. BIPES BIPORUS Cope

In *B. biporus* there are 150 vertebrae: 4 belong to the cervical portion, 124 to the thoraco-lumbar region, 3 to the cloacal region and 19 to the tail. The atlas consists of 3 elements. The two neurapophyseal pieces are larger than those of the axis. The third ossification connects the ventral tips of the arch pieces. The axis is relatively small, hardly larger than the following vertebrae. As in *A. fuliginosa* there are 2 hypapophyseal processes. These are tooth-shaped and point backward. At about the borderline between the axis proper and the odontoid process there is a prominent lateral tuberosity. The posterior edge of the neurapophysis is concave. The remaining neck vertebrae have strong hypapophyses; in the thoracic region they are absent. The tendon processes of the ribs face backward. The first cloacal vertebra has a pair of normally forked ribs, the two following vertebrae deeply forked transverse processes. All three cloacal vertebrae have "haemapophyseal" stumps that are ventrally enlarged in the antero-posterior direction. The transverse processes of the tail vertebrae face forward, the "haemapophyseal" arches backward.

Sternum, shoulder girdle and front limbs as well as the vestiges of the pelvis and rear extremities are adequately described in the general discussion, page 768 ff.

e. BIPES CANALICULATUS Bonnaterre

Fig. 3

B. canaliculatus has a shorter vertebral column (132-133 vertebrae) than *B. biporus*. The neck consists of 4, the thoraco-lumbar region of 102, the cloacal region of 4 and the tail of 22-23 vertebrae. The tendon processes of the ribs appear to be weak or absent except in the anterior part of the thorax. Few details can be made out with certainty from the x-ray plate concerning the cloacal region. Four vertebrae appear to belong to this region; the first one, probably, has a pair of forked ribs.

Shoulder girdle and front limbs seem to be very much like those of *B. biporus,* except that possibly finger no. 5 might be more weakly developed than in the compared form. Hobart Smith[9] states that he had examined 15 specimens of this species from Guerrero, Mexico, and observed that 2 possessed claws on the fifth digits, while the other specimens lacked them. A patella alnae as described on page 770 is also present in this species. Also the remains of the pelvic girdle and the hind limbs appear to resemble very closely those of *B. biporus*. On a different x-ray plate (not reproduced here) two elements can be made out on the same side of the animal. These undoubtedly correspond to the 2 principal elements (ilium and femur) in *B. biporus*.

f. GEOCALAMUS ACUTUS Sternfeld

Geocalamus has 134-135 vertebrae. Three belong to the neck, 106 to the thoraco-lumbar region, 4 to the cloacal series and 21-22 to the tail.

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9 By personal communication.

The atlas is made up of the 2 arch pieces and a tiny ossification (perhaps only calcification) in the hypocentral cartilage bar. The odontoid process of the axis is large, about twice as wide as the centrum; both hypapophyseal processes are present, but small. Prominent tuberosities to which strong muscles are attached are located to either side of the base of the odontoid process. The hypapophyseal crests of the third cervical and first thoracic vertebrae are very inconspicuous. The tendon processes of the ribs are slender and point upward and backward. The first cloacal vertebra has a pair of but faintly forked ribs. The dorsal limbs of the forks are small. The remaining 3 vertebrae of this region possess deeply forked transverse processes. The last 2, furthermore, have pairs of short ventral processes. The latter are quite large and ventrally united in all but the last few caudal vertebrae. The transverse processes of the tail vertebrae point forward except in the first two elements of the series where they stand at a right angle to the longitudinal axis of the body.

g. TROGONOPHIS WIEGMANNI Kaup

Of all the forms herein studied, *Trogonophis* has the shortest vertebral column, 89 vertebrae: 2 neck, 72 thoraco-lumbar, 4 cloacal and 11 tail vertebrae. The atlas consists of relatively large arch pieces, ventrally connected by a strong hypocentral ossification. The latter has a midventral, short hypapophyseal process. The neurapophysis of the axis appears drawn out into a long caudad process which nearly covers the neurapophysis of the following vertebra. The odontoid process is very wide, but relatively short. There is only one hypapophyseal crest, probably equivalent to the two of other forms, since it extends over the territory of both processes in other species. A lateral tuberosity at the base of the odontoid process is present. The last cervical and the first 4 thoracic vertebrae have strong hypapophyseal crests decreasing in size

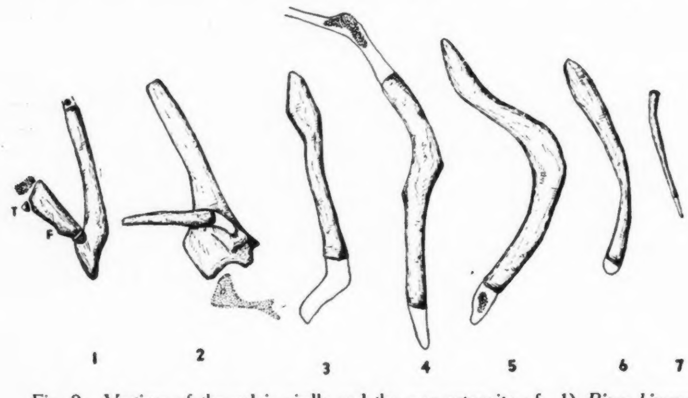

Fig. 9. Vestiges of the pelvic girdle and the rear extremity of 1) *Bipes biporus*, 2) *Blanus cinereus*, 3) *Leposternon microcephalum*, 4) *Rhineura floridana*, 5) *Amphisbaena fuliginosa*, 6) *Monopeltis c. capensis*, 7) *Amphisbaena ewerbecki*. About 12 times nat size. F, femur; T, tibia.

towards the back. The tendon processes of the ribs are strong and face backward. The cloacal and tail regions are like those of *Geocalamus acutus* in every detail. The ribs and processes are much stronger, however, and all the transverse processes of the caudal vertebrae point forward.

h. RHINEURA FLORIDANA Baird

Among the species observed, *Rhineura* possesses the greatest number of vertebrae, namely 155 or 156. There are 2 in the neck, 133 in the thoraco-lumbar region, 3 constitute the cloacal region, and 17 or 18 the tail. In this form only the arch pieces of the atlas are ossified. They resemble essentially those of *Amphisbaena fuliginosa*. The axis, on the other hand, is fairly characteristic. The odontoid process is but half the length of the centrum proper. The neurapophysis is relatively high and its posterior margin is moderately crested and bluntly pointed backwards. No hypapophyseal process originates from the dens epistrophei; a hypapophyseal leaf extends from the body of the axis proper. Along the ventral edge of the neurapophysis there are several minor crests, and a prominent tuberosity. The articulation surface of the dens is distinctly saddle-shaped. The first 3 thoracic vertebrae carry very thin, blade-like hypapophyses. The tendon processes of the ribs of *Rhineura*, absent in the posterior part of the thoraco-lumbar region, face forward. In this feature *Rhineura* differs from all other forms studied. The first cloacal vertebra (Fig. 4) has a pair of forked ribs, whereby the limbs of the forks are of about equal length, the 2 remaining vertebrae of this region have normally forked transverse processes. "Haemapophyseal" processes do not occur in the cloacal region, but are well developed in the tail. Occasional irregularities include the fusion of these processes of 2 adjoining vertebrae. The transverse processes of the caudal vertebrae are relatively short, but sturdy and stand at right angles to the longitudinal axes of the vertebrae. The pelvis vestiges (Figs. 4 and 9) on either side of the body consist of slender, slightly curved, bony bars. These are proximally and distally prolonged by cartilage rods that appear calcified on one side of the individual (Figs. 9 and 3).

i. MONOPELTIS C. CAPENSIS Smith

One hundred and ten or 111 vertebrae form the column of this form. The neck consists of 3, the thoraco-lumbar series of 94, the cloacal region of 4 and the tail of 8 or 9. The characteristic development in width of the skull of *Monopeltis* (Zangerl, 1944) is also reflected in the vertebral column, particuarly in the atlas and axis. Two rather delicate pieces form the neurapophysis of the atlas and a small ossification is found in the hypocentral cartilage. The atlas ring is at least twice as wide as it is long. The axis is somewhat unusual because of the lateral crests which form wide, horizontal wings with tuberosities below their anterior ends, and the neurapophysis that has anteriorly an indication of a processus spinosus. From this point it gradually gains height towards the posteriorly convex margin. There are two hypapophyseal processes, both faintly forked distally. The anterior one is minute in size. The odontoid process is relatively short, but almost as wide as the axis with its broad lateral wings. Hypapophyses are present on the third neck vertebra and on the first

2 thoracic ones. The tendon processes of the ribs are weak. The cloacal region consists of 2 vertebrae with forked ribs and 2 with normally forked transverse processes. In the ribs of the first cloacal vertebra the dorsal limbs of the forks are shorter than the ventral portions. Short "haemapophyseal" processes occur on all cloacal vertebrae and those of the tail where they are large and bent caudad. All the transverse processes of the tail vertebrae face forward. The pelvis vestiges of this form are small, slightly curved bars that are somewhat thickened near the proximal ends (Fig. 9).

k. LEPOSTERNON MICROCEPHALUM Spix

This form was only partially studied. The cloacal region includes 5 vertebrae. Only the first one of the series has a pair of forked ribs, the rest carry normally forked transverse processes, and "haemapophyseal" stubs which increase in length towards the tail. All of these processes point forward, whereas those of the tail region are bent backward. The pelvic vestiges are relatively short, club-shaped elements (Fig. 9) distally elongated by cartilage rods that are sharply bent caudad.

l. ANOPSIBAENA KINGII Bell[10]

The vertebral column consists of a total of 120 vertebrae besides an undeterminable number of fused ones at the tip of the tail. There are 3 cervical, 109 thoracic, 3 cloacal and 5 clearly defined caudal vertebrae. The atlas consists of the two neurapophyseal pieces only and these are not fused dorsally. The axis has 2 hypapophyseal keels whereas the 4 following vertebrae have one each. The vertebrae in the anterior part of the thorax are much wider than long; in the posterior part they are longer than wide. Several ribs appear to have been fractured in life and the fracture points are well marked by relatively large callus formations. The cloacal region is not as clearly defined as in other forms. Vertebra No. 110 has a pair of almost straight unforked ribs, the following two vertebrae have forked transverse processes and "haemapophyseal" stumps. All the tail vertebrae with the exception of the urostyle complex have relatively large "haemapophyses."

The shoulder girdle is represented by an exceedingly tiny bone on either side of the body at the level of the axis. The length of these vestiges is no greater than the distal diameter of an average sized rib. They probably are homologous to the scapulo-precoracoids of other amphisbaenids.

The pelvis was described by Smalian (1885) as consisting of two small rods, each bent at mid-length, somewhat broad in front and rounded in the back. In the present specimen the two little bones are evenly curved, of about equal diameter and each has a small process of calcified cartilage attached to it anteriorly. There is no connection between these bones and the cloacal region of the vertebral column.

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10 The description is based on a specimen (A.M.N.H. No. 17024) from Cordoba, Argentina. The specimen was cleared without removal of the viscera or the skin.

m. BLANUS CINEREUS Vandelli[11]
Fig. 7 and 9

The vertebral column of *Blanus cinereus* consists of 141 vertebrae and a coccygeal complex of about 3 elements. There are 3 vertebrae in the neck, 114 in the thoraco-lumbar region, 4 constitute the cloacal series and 20+3 (?) make up the tail.

The atlas has a small ossification in the hypocentral cartilage bar. The odontoid process of the axis is moderate in size and somewhat conical with its apex pointing cranio-dorsad. Hypapophyseal keels are present but weak. The tendon processes of the ribs are small and point dorsad. The first cloacal vertebra has a pair of very short, unforked ribs. The next vertebra possesses strong, but unforked transverse processes. The latter are deeply forked in the last 2 vertebrae of the cloacal series. In the tail region all the transverse processes are somewhat forked distally. Only the caudal vertebrae have "haemapophyseal" processes, and, all but the last pair are ventrally fused. The girdle and limb vestiges are described on pages 769 and 772.

Morphological Conclusions

The organization of the post-cranial skeleton of the Amphisbaenidae presents great uniformity. The specific differences described above do not even superficially obscure the typical "Bauplan" of the group. So far as this writer can see there are no intermediate forms among the lizards or the snakes which would suggest a closer morphological relationship of the amphisbaenids with either group. Individual features of amphisbaenid organization, however, are seen in some representatives of both lizards and snakes. The integument of the nearly limbless *Ophiognomon abendrothi* and the great length of the thoraco-lumbar region of *Aprasia repens,* e. g., at least superficially resemble the typical condition in the Amphisbaenidae, and so do the general body proportions of *Leptotyphlops d. dulcis.* Besides these superficial similarities there are important features which the amphisbaenids have in common with the lizards on the one side and with the snakes on the other (see Introduction, page 764). All these similarities are not necessarily indicative of a closer morphological relationship of the Amphisbaenidae with the Squamata, but can easily be explained by assuming convergent development.

Since the exact systematic position of the Amphisbaenidae remains to be determined, it is here suggested that the group be placed "incertae sedis" with the Squamata. The osteological characterization of the groups is as follows:

Skull relatively small enclosing a large cranial cavity; floor of the braincase at the same level as the floor of the cavum nasi; side walls of the orbitotemporal region of the braincase closed by pleuro- and orbitosphenoids; no columella cranii; stapes attached to lateral face of mandible by extracolumella and ligament or ligament only; facial part of skull usually bent ventrad; orbits very shallow, dorsally, ventrally and posteriorly open; dentition variable but always with a large, unpaired premaxillary tooth; quadrato-articular joint usual-

11 The description is based on a specimen from Spain (C.N.H.M. No. 603).

ly in a forward position; vertebrae procoelous throughout; thoraco-lumbar region very long, tail very short; cloacal region with usually one distally forked rib and several forked transverse processes; long, paired, ventral "haemapophyseal" processes in the tail region; axis and several following vertebrae with hypapophyseal keels; shoulder girdle and fore limbs usually vestigial, except in *Bipes;* shoulder girdle consisting of scapulo-precoracoid and clavicle; carpus lacertiloid; phalangeal formula: 3, 3, 3, 3, 3; pelvis and rear limbs always vestigial.

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A Technique for Analysis of Population Density Data

Ralph O. Erickson and John R. Stehn

The problem of the distribution of individuals of a plant species within a community has not received the same amount of attention as other ecological problems, such as those of recognition and classification of ecological formations, and of plant succession. Ashby (1936) has discussed some of the difficulties of the problem, and has reviewed the statistical methods which have been applied. Blackman (1935) has studied the distribution of a number of plants in grassland, and has attempted to fit the Poisson curve to the distribution of those plants which could be scored as discrete individuals. By the use of χ^2 test he has demonstrated that the "common" plants conform well with the random (Poisson) distribution, while "occasional" species do not. In at least one instance he attributes the lack of randomness, or correlation in occurrence of the plants, to the fact that vegetative reproduction occurs. Clapham (1936) has analyzed data collected by Steiger (1930) on the distribution of plants on high and low prairie, using relative variance as an index of over- or under-dispersion. He has found that the majority of the plants studied by Steiger show marked aggregation or over-dispersion, and has pointed out that, as a result of the over-dispersion of many plants, their mean density does not have much ecological meaning. Ashby (1935) has proposed using a quadrat consisting of a lattice of 16 or 25 squares, and counting the number of plants in the quadrat and the number of empty squares. If the distribution is random, the expected number of empty squares can be calculated from the number of plants in the quadrat. When the distribution departs significantly from random, a correction factor may be applied to make the observed number of empty squares agree with the calculated. The correction factor is a measure of the departure from random.

Elton (1932; 1933) has pointed out the necessity, in critical studies of population densities of an animal, of recognizing "blanks" or areas not suited for the animal, and excluding them from the area used in the calculation of density. For a density calculated in this way, he has proposed the term "economic density," as contrasted with a "noneconomic density," which includes areas not suited to the animal, or on which it does not occur. Mohr (1943) has reviewed small mammal censuses with the aim of determining by a consideration of the way in which they were taken, whether they yield economic density values or not. This concept apparently has not entered as specifically into plant ecological thought, though one finds differences in microclimate, soil, etc., suggested as factors in the departure of plant distribution from random. In the present paper, a statistical method is discussed and illustrated which permits an estimate of economic density to be derived from noneconomic data.

A field study is being made of *Clematis Fremontii* var. *Riehlii,* a plant which is restricted to an area of roughly 500 sq. mi. in east-central Missouri

(Erickson, 1943). It is entirely limited to glades, well-defined barrens occurring principally on the south- and west-facing slopes of otherwise wooded ridges (Erickson, Brenner and Wraight, 1942). A remarkable feature of the glades is the definiteness of their outlines. Since there is seldom any trouble in the field in deciding within a very few feet where the glade ends and the woods begin, and since the plant often appears to be "abundant," it might be supposed that a glade could be regarded as a uniform habitat for the plant, and that its distribution would be random. The numbers of plants occurring in 10-ft. quadrats have been scored on a number of glades. The quadrats constituted a series of 10-ft. transects laid out across each glade, usually at 250-ft. intervals. A careful preliminary study showed that there is practically no clonal reproduction, the variation from plant to plant being sufficient to allow the recognition with considerable certainty of presumed genetic individuals. The *Clematis* is perennial and shows great variation in size, depending upon its age; the plants have been scored as individuals regardless of their size. When the frequency of quadrats containing 0, 1, 2, . . . plants is plotted for a glade, a distribution curve is obtained which invariably fails to conform to the Poisson distribution, showing the phenomenon which Clapham (1936) has called over-dispersion. However, it has been possible to fit the data in most cases by calculation of two Poisson curves. The hypothesis is made that a glade may be separated into two components, one which is suitable for the plant, and one which is less suitable, or has not been colonized; and a theoretical distribution on each portion of the glade is calculated.

If the Poisson distribution function

$$y = Ne^{-m}\ m^x/x!$$

is written in the form

$$x!y = Ne^{-m}\ m^x$$

and the logarithm of each term is taken, one obtains

$$log\ (x!y) = log(Ne^{-m}) + x log\ m.$$

This is a linear equation, $log\ (Ne^{-m})$ being the intercept on the axis of $log(x!y)$, and $log\ m$ the slope. (In our example, x is the number of plants occurring in a 10-ft. quadrat; y, the number of quadrats containing x plants; N, the total number of quadrats; m, the mean number of plants per quadrat.) A test of the conformity of a set of data to the Poisson distribution may be made by plotting $log(x!y)$ against x (or on semi-logarithmic paper, by plotting $x!y$ on the logarithmic axis, against x on the linear), and attempting to fit a straight line to the points. An example of the goodness of fit that may be obtained is shown in Fig. 1, a graph of a sample of 96 data drawn in random fashion from an artificially made-up universe whose distribution was Poisson in type, with a mean value, m, of 3.50. The slope of the best-fitting line (dashed line in Fig. 1) drawn by eye in ignorance of the true distribution, is 0.570, corresponding to a value of 3.72 for m. The intercept on the vertical axis is 0.36, which leads to a value of 93 for N. For comparison, the theoretical line, corresponding to $N = 96$ and $m = 3.50$, has also been drawn (solid line in Fig. 1).

Even if the population from which the sample is drawn does not obey a simple Poisson distribution (and this is the case with the data on *Clematis*), a graph made in the manner described above may yield significant information. It may show, for example, that the points lie near a straight line for a limited range of values of x. Then one may conclude that the distribution has at least some Poisson characteristics. One interpretation might be that the data were drawn from two or more component populations, one of which obeyed the Poisson distribution. The straight line fitting a portion of the graphed data could then be extended, so long as it did not lie significantly above any of the data points, and it would represent that component population which was of Poisson type. The slope and intercept of the line would, as above, yield an estimate of the mean value, m, of the component population, and of the size, N, of the portion of the sample drawn from it.

Assuming that the above procedure has given a reasonable break-up of the data into two portions, one may then remove from the observed data that part which is the "known" Poisson one, and may make a fresh study of the remaining data. One may even use the same technique on the remaining data. This has been done for the data on *Clematis*.

The method of fitting the *Clematis* data is illustrated in Table 1 and Fig. 2. The first two columns of the table are field data from a glade near Hillsboro, Mo. The third column is obtained by adding $log(x!)$ and $log\ y_0$. When the data of the first and third columns are plotted (Fig. 2) it is seen that they approximate a straight line for the larger values of x. Fitting a straight line to

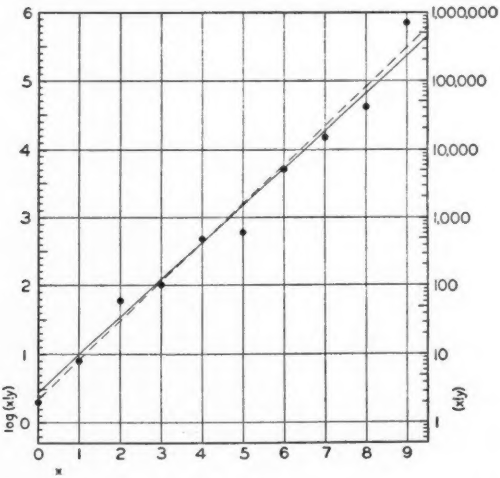

Fig. 1. Artificially made-up Poisson distribution, illustrating method of fitting with a straight line. Explanation in text.

TABLE 1.—Distribution of *Clematis Fremontii* var. *Riehlii* in 10-ft. quadrats on glade in Jefferson Co., Mo. (R.4E,T.40N,S.15) fitted with two Poisson curves.

x	y_0	$\log(x!y_0)$	y_1	(y_0-y_1)	y_2	y_{12}	(y_0-y_{12})	$\frac{(y_0-y_{12})^2}{y_{12}}$
0	176	2.2455	0.98	175.02	175.02	176.00	0.00	0.00
1	38	1.5798	3.81	34.19	34.21	38.02	–0.02	0.00
2	11	1.3424	7.37	3.63	3.34	10.71	0.29	0.01
3	9	1.7324	9.51	–0.51	0.11	9.62	–0.62	0.04
4	10	2.3802	9.20			9.20	0.80	0.07
5	9	3.0334	7.12			7.12	1.88	0.49
6	2	3.1584	4.60			4.60	–2.60	1.46
7	2	4.0035	2.54					
8	2	4.9066	1.23					
9	1 } 5	5.5598	0.53 } 4.60			4.60	0.40	0.03
10			0.21					
11			0.07					
12			0.02					
	260		47.2		212.7	259.9		2.10

$$m_1 = 3.87;\ m_2 = 0.195;\ \chi^2 = 2.10;\ P(\chi^2 > 2.10)_{n=4} = 0.71$$

these points is done in two steps. A line is drawn by eye (dashed line in Fig. 2) as a first approximation, and frequencies, y, for the 0-, 1-, and 2-classes are calculated from it. These estimated frequencies are used with the frequencies, y_0, observed for the 3-, 4-, 5-, . . . classes to find the total, N_1 and the mean, m_1, of the component Poisson distribution, represented by the solid line in

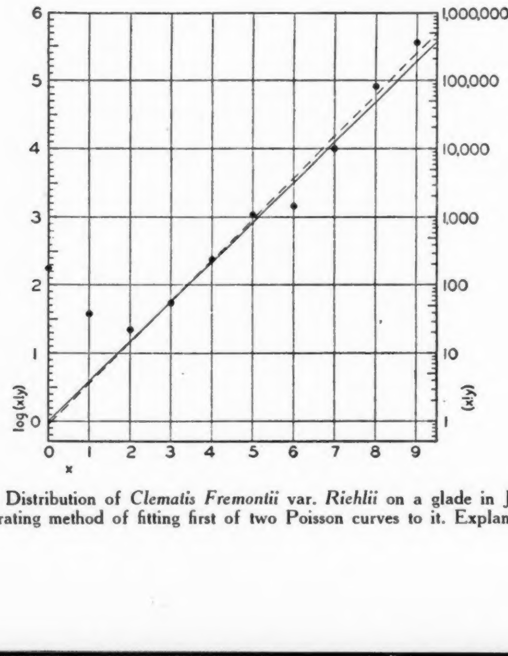

Fig. 2. Distribution of *Clematis Fremontii* var. *Riehlii* on a glade in Jefferson Co., Mo., illustrating method of fitting first of two Poisson curves to it. Explanation in text.

Fig. 2. The theoretical frequencies, y_1, are calculated from N_1 and m_1, and entered in the fourth column of the table. This may be termed the "economic distribution." It describes the distribution of the plant on the postulated favorable portions of the glade. Its mean can probably be fairly compared with Elton's "economic density."

In the next column the data for the less favorable portions of the glade have been estimated as the differences, $(y_0\text{-}y_1)$. These differences are significant only for $x = 0$, 1 and 2; and they comprise the remaining distribution. This also appears to be Poisson in type. Since there were so few classes, a simpler scheme was used for estimating its constants. The total number, N_2, was estimated as $(N_0\text{-}N_1)$; the mean, m_2, was calculated by assuming the difference $(y_0\text{-}y_1)$ for $x = 0$ to be 175.02, exactly what it should be for its distribution, in other words, to be unaffected by random fluctuations. This difference should be given by the expression $log\ (N_2 e^{-m_2})$, or $log\ N_2 - m_2\ log\ e$. Since N_2 has been estimated, m_2 can be calculated from the first entry in the $(y_0 - y_1)$ column. Frequencies, y_2, for this distribution are entered in the table. The term "adventitious distribution," is proposed for this curve.

The frequencies of the economic and adventitious distributions, y_1 and y_2, are added, and the χ^2 test is applied to test the agreement of the combined frequencies, y_{12}, with the field data, y_0. Fitting the two lines is equivalent to fixing the mean and total for each distribution, or four separate quantities. Hence, the number of degrees of freedom is reduced by four, and the χ^2 table is entered at $n = 4$. The probability for a greater value of χ^2 is 0.71, on the hypothesis of two Poisson distributions. This indicates a satisfactory fit.

TABLE 2.—Distribution of *Clematis Fremontii* var. *Riehlii* on several glades in Franklin Co. and Jefferson Co., Mo.

No.	Location	N_0	m_0	$\frac{\sigma^2}{m_0}$	Economic Distribution N_1	m_1	Adventitious Distribution N_2	m_2	χ^2	P
1	R.2E,T.42N,S.10	1012	0.57	1.37	590.3	1.02	421.7	0.007	0.28	0.55
2	R.2E,T.42N,S.15	234	1.16	2.99	50.4	3.61	183.1	0.471	3.34	0.34
3	R.3E,T.41N,S.25	552	0.41	2.77	50.0	2.98	501.9	0.142	9.21	0.03
4	R.4E,T.40N,S.15B	260	0.86	3.30	47.2	3.87	212.7	0.195	2.10	0.71
5	R.4E,T.40N,S.15D	258	2.05	4.52	(94.3	4.79 4.07	163.0	0.405	27.99	0.001)*
6	R.5E,T.40N,S.13A	96	0.34	1.69	30.0	1.10	66.0	0.000	1.04	0.32
7	R.5E,T.40N,S.13E	72	3.69	3.56	(41.8	5.90 2.51	30.2	0.583	18.31	0.006)*
8	R.6E,T.39N,S.4	376	2.85	1.99	276.7	3.76	99.3	0.371	6.47	0.26

* These two distributions are not satisfactorily fitted. They may be fitted with three Poisson curves.

Data on the distribution of *Clematis Fremontii* var. *Riehlii* on several other glades, all that have been investigated so far, have been fitted in this way (Table 2). The mean density, m_0, and variance ratio, σ^2/m_0, as calculated by Clapham, have been included for comparison. The χ^2 test indicates that all

but two are satisfactorily fitted as double Poisson distributions. These two have been fitted, in much the same way, with three Poisson curves:

No.	Location	N_1	m_1	N_2	m_2	N_3	m_3	χ^2	P
5	R.4E.,T.40N.,S.15D	11.0	14.27	77.7	4.07	169.3	0.443	12.23	0.10
7	R.5E.,T.40N.,S.13E	21.0	8.36	36.9	2.51	14.1	0.000	1.81	0.88

These two glades show signs of having been disturbed. While no direct evidence is at hand, it is suspected that they have recently been released from severe grazing, since both were characterized by the presence of "weed" species. An unusual number of small, sterile *Clematis* plants were found on both glades. The second mean, m_2, is regarded as most nearly characteristic of these two glades, and it has been inserted in the m_1 column of Table 2. It will be seen from Table 2 that the economic density, m_1, is a somewhat more consistent estimate of population density than that obtained merely by dividing the total number of plants by the number of quadrats. It should be pointed out that glades 1 and 6, with low economic density values, m_1, are much smaller, and more inaccessible glades than the rest. Glade 1, particularly, was remarkable for the large size of its many red cedars, *Juniperus virginiana.*

This method of fitting has been applied to Blackman's (1935) data on *Primula auricula* and *Plantago media,* as read from his Figs. 3 and 4, respectively. *Primula auricula* has an economic density of 3.49 plants per quadrat, with a probability for χ^2 of 0.23. That of *Plantago media,* obtained by combining his four distributions, is 2.19, with a probability of 0.17. Some of Steiger's (1930) data can be fitted, but the method fails with many of the plants he has studied. In these cases, clonal reproduction is probably an important distributional factor. The method also fails with Epling and Dobzhansky's data (1941; and letter of Aug. 26, 1943) on *Linanthus Parryae,* although vegetative reproduction is said to be absent in *Linanthus.* The method can probably be applied only to plants in which vegetative propagation is not important. It is a method for separating statistically the favorable portions of the habitat, when that separation is impracticable in the field, rather than a method for dealing with the problem of aggregation as a result of vegetative reproduction.

The division of the distribution of the *Clematis* into two components is admittedly an artificial device. Field experience on the glades suggests that it would be more reasonable to consider the distribution to consist of a continuous series of Poisson distributions, corresponding to a continuous variation in the suitability of various portions of the glade to the plant. However, the hypothesis implicit in the method seems to be a fair approximation to the truth, and the method is a useful one.

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Evolution, Succession, and Dispersal

Karl P. Schmidt

Coming to the study of ecology from long specialization on the systematics of the living reptiles, and with the background of a travelled naturalist, and thus to a belated reading of ecological literature, I stumble over Shelford's statement in *Physiological Animal Geography* (1911, p. 554)[1] that "The study of physiological animal geography may be conducted independently of the problems of evolution." In his definitions of both faunistic animal geography (which he finds outmoded) and the new "physiological animal geography," I find no mention of adaptation, or of the origin of adaptation. Of the ecological phenomena that justify the establishment of ecology as a department for independent research, none seems more impressive than the observable succession of biotic communities. I detect from conversation with my colleagues, with some amusement at the prevalence of fashion as a motive in University research, that the study of succession is now regarded in some circles almost as an "überwundener Standpunkt."

The rejection of evolution as an essential basis for the examination of ecological phenomena seems to me to be merely a wilful avoidance of the complexity introduced into ecological concepts by evolution, and no more defensible than a similar attitude on the part of a physiologist or embryologist who deals with other resultants of evolution. The concepts fauna and flora (and biota), are replaced in ecological investigation by the useful concepts of the animal community and the biotic community, but apparently without much attempt at correlation with the older terms.

In order to clarify my own thinking with respect to succession, adaptation to life in the specific habitats that may form transient elements in the successional series, and the phenomena of dispersal, I have prepared the accompanying diagram. In simplified form (doubtless oversimplified) this diagram attempts the correlation of the evolutionary concept of a process of continuing adaptation to a specific habitat niche with the now familiar concept of ecological succession, which assumes the existence of adapted plants and animals.

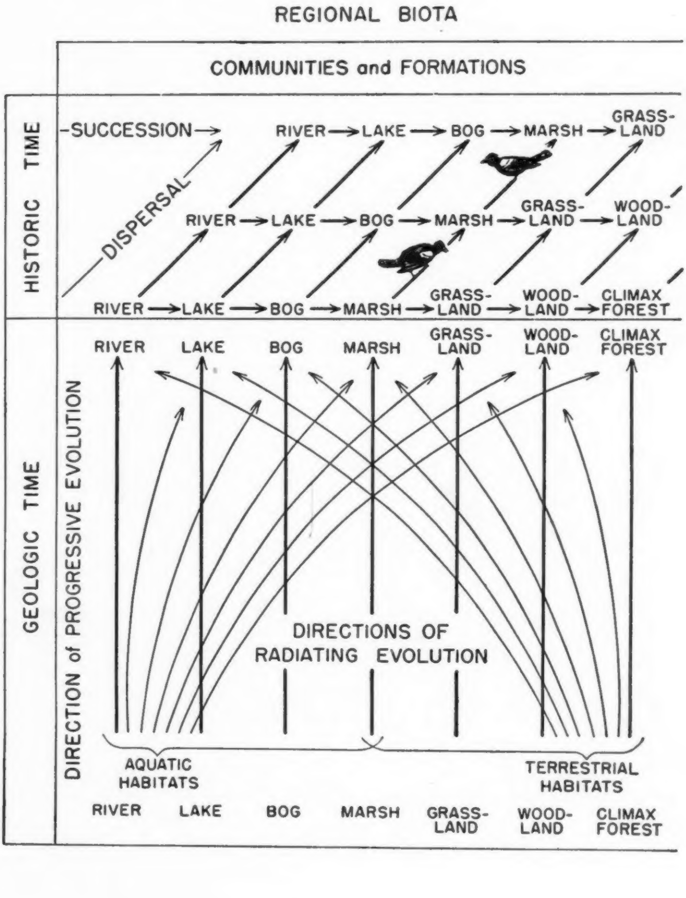
The time element in the successional stages is too short for the ordinary operation of evolutionary change; for this reason *dispersal* ordinarily proceeds from aquatic habitat to aquatic habitat, or from a single type of habitat like marshland to similar marshland, rather than in the direction of succession. Such dispersal obviously makes possible the perfection of adaptation to a specific habitat.

The essence of the concept of distinct biotas characterized by endemic forms is that they result from isolation through geologic time. This is sufficiently evident in the case of long isolated large islands. When the isolation is in an area in which the limiting factors are themselves biotic or in part

1 Jour. Morph. **22**:551-618.

biotic, the relation becomes less and less evident in inverse ratio to the duration of the time during which the factors have continued in operation.

Major physiographic and climatic changes affect the whole biota, including all of the successional stages and fresh-water life equally with land life. Such changes are geological phenomena, and the biotic regions of the world accordingly rest on a long-term historic basis. *Endemism,* the basis of faunal and floral regions, is geographic and historic, and *not* ecological or successional. Adaptation to an ecological formation that may be distinctively subject to succession, is essentially an evolutionary and historic phenomenon. The complexity introduced into biological thought by the phenomena of evolution is



further illustrated by radiating evolution, in which living organisms adjust themselves to life in new habitats quite without reference to the direction of succession, and quite evidently in relation primarily to the existence of surpluses of food. The essentially riparian turtles, which have been a recognizable group since the beginning of the Triassic, illustrate the several phenomena under discussion. The typically riparian forms disperse to new river banks or new marshes when the old ones are converted to terrestrial habits. In the course of their continuing evolution in this habitat they have become increasingly adjusted to it. The evolutionary direction into permanently aquatic life is illustrated by numerous independent lines arising in the Age of Reptiles, such as the soft-shelled turtles in fresh water and the several groups of marine turtles. The contrary direction, of permanent adjustment to terrestrial life, and even to life in the desert, is equally well exemplified by the land turtles of the genus *Testudo* and its close relatives. The intermediate stages are obvious in the wood turtle (*Clemmys insculpta*) of eastern North America and in the Oriental genus *Cyclemys*. It is not the purpose of the present paper to amplify illustration of the phenomena represented by the lines of the diagram, but rather to offer it to my critical colleagues for comment and dissection.

Substrate and Movements of the Marine Gastropod Acmaea asmi

Frederick H. Test

The limpet *Acmaea asmi* Middendorff is a small, black-shelled, marine snail occurring on the west coast of North America. Its geographical range is given by Oldroyd (1927) as "Sitka, Alaska, to San Diego, California, and Socorro Island, Lower California." At Moss Beach, San Mateo County, California, where the following observations were made in May and June, 1937, *A. asmi* occurs as a common inhabitant of the intertidal zone, particularly the more protected regions of the upper part. The shell is dull black, with fine striations radiating from the apex and often slightly roughened externally by a fungus. Shells of large adults measure about 6.0 mm. by 4.5 mm. by 4.0 mm. high. The shell is not coiled and is subconical in shape, with the apex slightly anterior to the mid-transverse plane of the animal.

In many types of studies dealing with natural populations of animals it is necessary to know something of the movements of individuals. This sort of information enters into problems of population changes, evolution, ecology, life history, and other types. The notes given below were recorded with the purpose of supplying information for this kind of problem. These observations are not a complete study, but opportunity for the writer to do further work on this animal is uncertain and at some distance in the future at best, hence the presentation of these notes at this time.

The movements of some of the larger species of *Acmaea* have been studied, but all of them occur almost exclusively on a rocky substrate. *Acmaea asmi* is unique among members of the genus in that it usually is found on the shell of another gastropod. Most commonly the host species is *Tegula funebralis*, a black snail with a coiled shell attaining a length of about 30 mm. and found in the upper intertidal zone. The rarity of occurrence of *A. asmi* on shells of another species of *Tegula*, *T. brunnea*, which occurs in the same locality, is perhaps a result, in part, of the greater wave action to which this *Tegula* is subjected in inhabiting the outer sides of the reefs. Another factor discouraging to *A. asmi* may be the thick coat of a velvety brown alga with which *T. brunnea* is usually encrusted. Individuals of *T. funebralis* with the same growth have never been found to bear *A. asmi*, in my experience. Rarely, I have seen *A. asmi* on shells of *T. funebralis* inhabited by hermit crabs (*Pagurus*), but never have I found *A. asmi* on shells of any other genus than *Tegula*.

Another location in which *A. asmi* has been found to be not uncommon is the bottom of small, rock-walled tidepools. In such situations, individuals occur in the angles of tiny ledges and crevices, and on the lower sides of loose, water-worn stones. In the laboratory, an individual of *A. asmi*, when placed on the bottom of a finger bowl filled with sea water, moved onto a nearby small stone within a few minutes.

The body whorl is the region of the *Tegula* shell usually occupied by *A.*

asmi. Rarely, one is found on the second whorl, but I have never seen an individual on the apex, which usually is much eroded. Notes made during low tide on an exposed reef in the course of a week of intermittent study of several marked individuals of *A. asmi*, *in situ*, indicate that a particular animal has no preferred position on the *Tegula* shell. Sometimes they occur on the upper side of the body whorl, sometimes on the lower side. Individuals of *A. asmi* over 3 mm. in length most commonly are found singly on *Tegula*, but sometimes there are two present. A single *Tegula* shell frequently bears more than two small *A. asmi*. The greatest number I have seen together is eight, of which two were over 3 mm. in length.

Movements of individuals were studied by marking them with yellow enamel paint. The animals to be marked were removed from the water on the shell to which they were attached, and their shells were dried with a cloth. A small serial number was then painted with a brush on the shells of both the *A. asmi* and its host *Tegula* and allowed to dry in the air for several minutes before the animals were returned to the spot from which they had been taken. Sometimes the numbers remained clearly legible for several days, but often it was impossible to identify them after twenty-four hours. Measurements taken of each individual at the time of marking aided in later identification of some animals from which part of the painted number had been lost.

Individuals watched in daylight in and near tidepools at low tide, when the adjacent parts of the shaley reef were emergent, moved about little. It is probable that there is more activity at night, as has been found in certain other species of *Acmaea* (A. R. Grant, MS.). When a *Tegula* crawls out of water, the *A. asmi* on it almost immediately pulls its shell down tight against the substrate. In moving, an *A. asmi* holds its shell about 0.3-0.5 mm. from the substrate, a habit which would allow considerable desiccation in air. It is, perhaps, because of this habit that I have seen no individuals move when out of water. Movement in water is relatively slow, usually, and in an exploratory manner. An individual with a shell length of 4 mm. moved at a rate of 1 cm. in forty-seven seconds in slightly warmed sea water in a Syracuse dish, immediately after being brought into the laboratory. The first direction assumed by an isolated *A. asmi* usually is maintained until an obstruction intervenes, but there are slight movements to either side as the animal progresses. Locomotion is not continuous for more than a few minutes; that is, activity occurs in spurts. As the animal moves, the tentacles are held forward or slightly back on the sides and are kept in almost constant motion, their tips against the substrate as though feeling the way.

Studies by Hewatt (1940), under both natural and experimental conditions, have indicated that individuals of a rock-inhabiting species, *Acmaea scabra* (Gould), frequently return again and again to the same place, usually a slight depression, to spend their quiescent periods. Observations on this and other rock-inhabiting species of *Acmaea* by Wells (1917), Richardson (1934), and Villee and Groody (1940) have shown that there is great irregularity in the return of individuals to the same spot, larger ones showing a much greater tendency to return than do small ones. It has also been observed that large individuals of certain species apparently tend to remain for many days in the same position in the same spot.

My observations on *A. asmi* show no tendency for individuals to remain on the same *Tegula* for more than a few hours, nor is their position on the *Tegula* shell other than temporary. For example, an *A. asmi* was marked while on a *Tegula* with a shell diameter of 14 mm.; it was on the body whorl just to the right of the aperture. The next day it was on an unmarked *Tegula* 15.5 mm. in diameter, at the posterior side of the body whorl. Another individual was watched as it glided over the shaley bottom of a small tidepool. As it came opposite, and 7 mm. from, a group of *Tegula funebralis* it hesitated, then turned toward them, at right angles to its previous course. On reaching the nearest *Tegula,* the *A. asmi* touched the edge of the shell with its tentacles before moving upward and continuing onto the second whorl. As it climbed the *Tegula,* the long axis of the body of the *A. asmi* was at a 30 degree angle to the line of motion. After a few minutes the *A. asmi* moved to the other side of the *Tegula,* which had remained stationary, and directly onto the shell of another *Tegula* in contact with the first. I have no record of an *A. asmi* remaining more than 24 hours on the same *Tegula.*

In nature I have not seen *A. asmi* move over a rock substrate for more than 15 cm. In most places they probably do not have to go farther than this before encountering a *Tegula.* One marked individual which was on a *Tegula* in a small tidepool was found the next day 25 cm. away and in another tidepool, on another *Tegula.* There was no way of learning how the limpet had moved from one place to the other, whether by its own locomotion or on a *Tegula.*

Two items are of special interest in the actions of the *A. asmi* mentioned in the second paragraph above. First, this is evidence that the group of *Tegula funebralis* provided a definite attraction for the *A. asmi.* From its actions, compared with those of individuals more or less isolated, there seems no doubt of the *A. asmi*'s "preference," at that time and place, for the *Tegula* rather than for the rock bottom of the tidepool. Second, the stimulation of the *A. asmi* is indicated to be through chemical means. It is probable that secretions or excretions reached sufficient concentration at a distance of 7 mm. from the group to stimulate the *A. asmi.* The *Tegula* were motionless at the time.

I am grateful to my wife, Avery R. Test, who has recently completed a systematic and biological study of the genus *Acmaea,* for a critical reading of the manuscript.

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Notes and Discussion

Notes on Foliar Dimorphism in Quercus nigra L.

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The common water oak (*Quercus nigra* L.) is one of the most widely known oak species in southeastern United States. Seedlings occur abundantly in sandy soil, swamps, river swamps, and often on slopes, in upland woods, near dwellings and along roadsides. These seedlings can be divided into two distinct groups on the basis of leaf shape (see Fig. 1). One type has leaves which are cuneate, cuneate-obovate to spatulate while the second type has a linear-lanceolate, linear—(or otherwise narrowly oblong) elliptic shape. Trees grown from both types of seedlings bear the broad leaves characteristic of this species. I have observed during the last fifty years that the broad-leafed seedlings are almost always regarded by other observers as water oaks, whereas the narrow-leafed forms are simply ignored or, if they are noticed, they are called willow oaks. Few observers have ever noticed that the narrow-leafed seedlings ultimately grow to be adult water oaks.

The cause of the different shapes of the juvenile leaves of the seedlings is unknown and for that reason attention is here called to this fact in the hope that some investigator will be attracted to the problem.

Fig. 1. *Quercus nigra* L.—Leaf contrast of a random pair of seedling plants, both about 5 dm. high and apparently of the same age. The broad leaf form represents the cuneate type, the narrow leaf form is representative of the linear type of seedling leaf shapes.

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Book Reviews

GASTROPODA. Von W. Wenz. Handbuch der Paläozoologie, Band 6, Teil 1 and 2. Borntraeger, Berlin, 1938. viii + 480 pp., 764 figs. RM 92.50.

"Gastropoda" is not only a successful compilation of the gastropod genera but treats also comprehensively the morphology and anatomy of the whole class. Thus it represents a type of work which is much needed for many other invertebrate groups and will therefore be welcomed by both zoologists and paleontologists.

The first 84 pages of the work are given over to a discussion of morphology and anatomy, ontogeny, physiology, ecology, phylogeny, general classification and a moderate bibliography. The remaining 156 pages of part 1 and all of part 2 deal with generic descriptions. In this volume Wenz has classified only the orders Archoeogastropoda and Mesogastropoda of the subcless Prosobranchia. Work on the classification of the Opisthobranchia and Pulmonata was obviously interrupted by war conditions, at least, the remaining parts of the work have not yet come to the reviewer's attention.

Paleontologists will be especially interested in Wenz's discussion of gastropod shell structure, the significance of the protoconch, the 35 pages on ecology, and lastly the classification; whereas, zoologists may be more interested in the chapters dealing with morphology and physiology.

The protoconch is considered to be of special importance in classification and description because it maintains throughout much of its development the phylogenetic coiling and consequently family relationships can be recognized even though the shell form later becomes modified. This is especially significant in the study of fossils. However, a warning is given to those who might exaggerate the value of the protoconch when it is known from only a single specimen. Large numbers of individuals from various habitats must be studied before its value in classification becomes significant.

The protoconch begins with a small more or less round nucleus. It usually shows the same type of spiraling as the other volutions, orthostropic or homeostropic, seldom the opposite or heterostropic.

It is pointed out that some gastropods remove themselves from the older volution by the construction of a cross wall or septum. This process is often carried out repeatedly and is most common in the turreted forms. Septum building has been recognized in several families among which are the Bellerophontidae and Euomphalidae. Indeed, a longitudinal section might have a strong resemblance to the transverse septa of a cephalopod.

The presence of an operculum in some of the gastropods is common and well known but the existence of a winter covering on some species consisting of a calcareous plate may not be such a well known phenomenon. On *Helix* it serves for protection during the winter and is cast off in the spring.

The operculum is constructed spirally or concentrically. Its outer margin is shaped so as to fit the aperture, but may be coiled in one or more volutions. It is usually thin and not often fossilized.

Coloring in gastropod shells is due to hematin, lipochrome, and melanin. These are usually destroyed during the process of fossilization but occasionally are preserved, especially in Cenozoic and Mesozoic material; melanin is the most commonly preserved. Use of ultra-violet light will aid in finding hidden color patterns.

The locomotion of gastropods is varied. They range from sessile to free-swimming forms. Though all marine forms are free-swimming in the larval stage this may represent a very short interval of time for a few species. Free-swimming pelagic forms, as the Bellerophontidae, are characterized by symmetrically coiled shells. Sessile forms are more apt to have the highly irregular coiling represented by the Vermitidae.

Sessile gastropods often develop enlarged apertures and soles which enable them to hold fast to an object and thereby remain almost stationary against swift currents or

strong waves. This is well illustrated in the recent and fossil Lymacidae and Neritidae.

Regeneration of parts is well developed in the gastropods. Small breaks in the shell are quickly repaired by the mantle. Damaged apertures can also be replaced. This sometimes results in double apertures.

Climatic conditions are important factors in the control of shell form. Dryness tends to develop thick white shells with narrow apertures. Animals with thin, transparent, smooth shells inhabit moist meadows; those with small shells live among the moss and grass with color bands developed in harmony with the surroundings.

The whole realm of habitats is discussed and the environmental control on the shape, form, and ornamentation of the shell is considered. The importance of temperature, depth, currents, composition of the water, moisture, nature of the floor, lithology of rock and vegetative association is pointed out. The importance of this section to studies of fossil faunas can be readily understood. Among many other things, Wenz notes that the greatest number of marine gastropods live on a rocky bottom. Here strong shells with wide flat apertures predominate. Gastropods are apt to disappear from strongly calcinated waters. The few that remain will develop abnormal shells.

One of the very valuable portions of the treatise is the table giving the geological range of each genus.

Each generic description is accompanied by data pertaining to number of known species. The 1235 illustrations are on the whole good.

It is to be regretted that such a thorough pice of work is not accompanied by an index. Lack of such will prove to be a great inconvenience. It is assumed that plans had been made for the inclusion of an index in the last issue on the class. Bibliographers may also find the policy of publishing Vol. 6, part 1, before the appearance of Vols. 1-5 confusing; especially if world conditions are such that the contemplated works on other groups are never completed.

The reviewer expresses appreciation for aid in translation to Miss Ellen Jordan.—HAROLD W. SCOTT, Department of Geology, University of Illinois.

THE APHIDIINAE OF NORTH AMERICA (BRACONIDAE: HYMENOPTERA). By Clyde F. Smith. Contributions in Zoology and Entomology, No. 6. Ohio State University, Columbus, Ohio, 1944. xii + 154 pp., 17 pls. (148 figs.). $3.50, cloth bound.

The Aphidiinae is a well-defined subfamily of Braconidae including small species parasitic exclusively on plant lice. Some are important agents in the biological control of economic pests. This book presents a taxonomic study of the species known from America north of Mexico and records their hosts and geographic distribution. Its author has reared specimens from a great number of plant louse hosts, has received material from many of the present generation of more active field entomologists, and has studied the material in the United States National Museum. Seventy-six species (twenty-eight of them new) and six genera are treated.

The keys and descriptions emphasize differences in wing venation, female and male terminalia, color, propodeum, length and number of antennal segments, and measurements of parts of the head and thorax. Male and female terminalia and front wings of most of the species are well figured and there are a number of figures of heads, propodeums, and petioles. All of these characters seem to have been carefully studied throughout the group but search for characters elsewhere seems to have been neglected. With a more careful study of morphological characters, knowledge of more species, and the use of host data Dr. Smith has made a notable advance in the classification of the subfamily. A new subgenus has been erected for two species of *Trioxys*, and *Aphidius* has been divided into five subgenera, among them *Lysiphlebus*, a group usually given generic rank. Altogether this is one of the best taxonomic studies of a group of Nearctic parasitic Hymenoptera that has appeared to date, but the small size and the difficulty of the species makes it inevitable that future studies will turn up many more species and additional characters which will further clarify the known species and their relationships.

Dr. Smith has evaded an important nomenclatorial problem. The genus *Aphidius*, proposed by Nees in 1818, is a strict synonym of *Incubus* shrank, proposed in 1802.

Few authors have used *Incubus* rather than *Aphidius* and Incubinae rather than Aphidiinae, but if rules of nomenclature are to be applied impartially there is no alternative. Aside from the preponderant usage of *Aphidius*, Dr. Smith's "reason" for not using *Incubus* is that the type specimen of its genotype, *Ichneumon aphidum* Linnaeus, is lost. It happens that the type specimen of *Bracon picipes* Nees, the genotype of *Aphidius*, appears also to be lost. Because both original descriptions are inadequate, the type species of either generic name must therefore be identified according to some reviser.—HENRY TOWNES.

AMPHIBIANS AND REPTILES OF THE CHICAGO AREA. By Clifford H. Pope. Chicago Natural History Museum Press, 1944. 275 pp., 12 pl., 50 Text Fig. $1.75.

Man's interest in nature is usually aroused by casual observations in his immediate surroundings. In large cities, however, the chances for such observations are relatively rare and in consequence, large sections of city dwelling populations never learn the art of accurately observing natural history phenomena and to appreciate their significance. It is, therefore, the explicit purpose of the present book to give a reliable account of what is known about the herpeto-fauna of the Chicago area within 70 miles of the city, and to stimulate the layman's interest and curiosity by suggesting the many details which are yet to be observed. Thus the reader, undisturbed by technical language, becomes the co-worker of the author.

The book is attractively printed and adequately provided with excellent illustrations and simple keys for the identification of the more than 50 species of amphibians and reptiles of the area. Each individual account covers such topics as recognition, sexes, reproduction, growth and age, habits, food, habitat, enemies, economic importance and occurrence. Reference works are added to the description of each species.

Amphibians and Reptiles of the Chicago Area is a carefully prepared book, enthusiastically written by a true naturalist; it can hardly fail to inspire its readers.—RAINER ZANGERL.

BIRDS OF THE SOUTHWEST PACIFIC. By Ernst Mayr. Macmillan Co., New York, 1945. xix + 316 pp., 16 figs., 3 col. pls. $3.75.

Designed as a handbook, this book fulfills a definite need for a brief, yet accurate, popular account of the birds of the Southwest Pacific. It is rather unique among handbooks, because of the wealth of previously unpublished material; it is not a mere compilation of the literature.

The book is divided into two major sections. Section one, the general section, deals with all of the seabirds and shorebirds and most of the widely distributed land and freshwater birds in the Southwest Pacific. The second section (geographical) treats by island-groups the land and freshwater birds which are more limited in their distribution. Consequently it is necessary to refer to four separate units of the book to build up a composite picture of the avifauna of any island or group of islands. This is not desirable, but as Mayr points out, it is a compromise to reduce the bulk and repetition which would be necessary if the book dealt with the birds of each group of islands as a separate unit.

The several keys are very useful, as is the system of cross-referencing of species. All material in the book is well-indexed. Literature citations are relatively few, but that is to be expected in a field book.

English vernaculars have been invented for more than half of the species. This seems unnecessary and confusing. Native names which are also included for some forms are often more useful in working an area since they frequently are already known by both native and transient persons interested in birds.

The figures are well-made, but there are too few of them for a book written for field identification. Smaller figures would have shown the diagnostic characters as well and would have permitted the use of perhaps twice as many illustrations. Very brief descriptions unaccompanied by drawings often make field identification difficult.

Inclusion of extinct forms (*Aplonis corvinus* and *Dendrocygma a. arcuata*, for example) appears to be out of place in a field book. Nonetheless, it may stimulate further search for rare and supposedly extinct kinds of birds.

"Birds of the Southwest Pacific" will prove useful not only to the amateur but also to the professional ornithologist for it is the only comprehensive book dealing with all of the birds now known from that region. It will encourage observation and collection in this part of the Pacific which is little-known to the average person.—HARVEY I. FISHER, Department of Zoology and Entomology, University of Hawaii, Honolulu.

INDIVIDUALITÄT UND FORTPFLANZUNG ALS POLARITÄTSERSCHEINUNG. By Armin Müller. Gustav Fischer, Jena, 1938. 66 pp. Paperbound. RM 3.00.

Dissatisfied with the inadequacy of current explanations given to the morphogenetic and causal aspects of the caudad (and ventrad) displacement of the gonads in higher mammals and Man, the author explores various other possibilities of interpretation and concludes that the problem is essentially physiognomic in character. Throughout a holistic point of view is maintained, inasmuch as the nature of morphological analysis of part of an animal is believed to contribute to the understanding of the development and structure of the whole animal. Form as such is reaffirmed in its organic unity and elevated to a pivotal position after all pertinent facts accumulated along diverse lines of biological investigation have been integrated. In his postscript A. Portmann points out that the author's ideas, exemplified by the special problem in question, are buildling stones in the development of future knowledge of animal forms which is expected to be more in keeping with the vast range of the subject rather than with the concepts in use so far.

Beginning with Heraclitus, who first formulated the concept of polarity, the author traces the recurrence of it in later philosophical writings and correlates these with the findings of modern biology and medicine. His appraisal of various "laws" and tendencies yields the following rather far reaching conclusions: the caudad (and ventrad) displacement of gonads is accompanied by a cephalad migration of important nerve centers closely connected with telencephalization; the mammalian body, more especially the human body, possesses a morphological pattern according to which the main body regions, particularly the central nervous system, show a correlation between position and "physiological valence," i.e., an axial gradient is evident whose frontal pole exhibits pronounced "physiological dominance"; as seen in regeneration phenomena, in the relationships of germ plasm and soma, etc. the antithesis between reproduction and all other functions increases with every step in the scale of classification; this antithesis is evidenced physignomically by the visible differences between the two poles.

Considering the high goal set here for morphology, the reader wonders about the real "explanation" of the phenomenon selected as a basis for this discussion. No doubt other organ systems and their relative displacements, too, might be subjected to similar analysis but most likely with different results. It seems, also, that the formalism of contrasting soma with germ plasm and reproduction with the sum total of other activities carried on by the mammalian body is no longer justifiable in the light of recent cytological findings. Even if this were so, how much more is actually gained toward a better understanding of animal forms than can be expected from the continued pursuit of all branches of biological research? Is it really easier to interpret the mammalian body largely in terms of polarity of certain systems and functions or has another unknown been added to the rather extensive list of those which still confront the morphologist? Polarity may well be an important attribute of many biological structures ranging from submicroscopic entities to whole organ systems in Man. Yet it is doubtful that it alone can be the key which will unlock all morphological riddles.—THEO. JUST.

DIE POLARITÄT DER PFLANZE ALS SCHLÜSSEL ZUR LÖSUNG DES GENERATIONSWECHSELPROBLEMS. By Hans André. Gustav Fischer, Jena, 1938. 86 pp. Paperbound, RM 3.50.

Written as a direct sequel to Müller's *Individualität und Fortpflanzun als Polaritätserscheinung*, this little book represents its botanical counterpart, as can readily be seen from some of the conclusions reached by the author. For example, the bipolar

structure of the phanerogamous embryo is a constitutional (autotropous) character and not the result of gradual adaptation. Therefore, he considers the autotropism of this bipolar axis as a striking parallel of the autotropous displacement of gonads in higher mammals. To the primary antithesis of *above* vs. *below* must be added a secondary one of *peripheral* vs. *central* (or leaf vs. shoot development). Flowers as well as inflorescences modify definitely the mode of branching of the bipolar axis. Leaf venation and phyllotaxy, too, disclose that this interference is polarized depending on whether indeterminate (racemose) or determinate growth prevails. The development of the vegetative shoot is, then, in some measure opposed to that of the flower or flowers but not a true indicator of polarity. The latter finds its best expression in the antithetic alternation of generations exhibited by many plant groups.

Despite earlier attempts by some botanists to interpret vegetative growth (development of individual plant) and reproduction (production of new individuals) as phenomena of polarity of primary significance, André apparently first thought of relating them to alternation of generations. The gradual reduction of the gametophyte, especially in vascular plants, is accompanied by the elaboration and expansion of the sporophyte, until the few celled gametophyte has lost virtually all other functions except its principal one, i.e., reproduction ensuring the largest number of possible hereditary combinations. Significantly, the spore mother cells, spores, and gametophyte are assigned by the author to the *analytical* generation concerned with "outbreeding," whereas the sporophyte (except the stages mentioned above) represents the *synthetic* one. Analogies based on physiological considerations (metabolism, particularly photochemical reactions and their uniformity among plants) are presented as evidence supporting these conclusions, while possible bearings of this polarity on other problems are freely suggested at the end of the book.

Phenomena of polarity in plants other than those treated in this book are numerous (see Bloch, R. 1943—*Polarity in Plants*. Bot. Rev. 9: 261-310. and Ungerer, E. 1926 —*Die Regulationen der Pflanzen.*) and have long been favorite subjects of botanical research. Also certain recent interpretations of alternation of generations have neither been discussed by André nor compared with his own views. It seems, therefore, that the author has given us a new approach to and many interesting observations regarding this fundamental problem but he has not resolved it.

Characteristically a holistic point of view pervades the book. This may account, in part at least, for the difficult style adopted by the author. At any rate, *Die Polarität der Pflanze* etc., must now be added to the rather short list of botanical contributions classifiable as holistic in viewpoint, a position which so far seems to have been largely assumed by embryologists and theoretical biologists.—THEO JUST.

LECTURES ON THE INORGANIC NUTRITION OF PLANTS. By D. R. Hoagland. Chronica Botanica Co., Waltham, Massachusetts. 1944. 226 pp., 28 plates, 44 figs. $4.00.

As indicated by the title this book is essentially a series of lectures given by Professor Hoagland (at Harvard University under the Prather Lectureship). As such the lines of research discussed are largely those with which the author has been more or less directly associated. Thus, as Hoagland indicates in the preface, the publication should serve to give perspective to several important aspects of inorganic nutrition but is not intended to be a comprehensive survey of the field. Although brief it is an excellent contribution which should be of considerable interest to students and workers of botany and agriculture.

The lectures, of which there are seven in all, average about twenty-five pages each and include a list of references. In the first lecture a survey is made of the broader phases of plant nutrition. Following a short historical introduction mineral nutrition is considered primarily as a process in a dynamic soil-plant-atmosphere system, the complexity of which is properly emphasized. In the remaining six lectures the following topics are discussed: micronutrient elements (with particular reference to zinc); absorption and accumulation of salts; movement and distribution of inorganic solutes in the plant; growth of plants in artificial media in relation to plant nutrition; biochemical problems associated with salt absorption; and aspects of potassium nutrition as illustrating

problems in the system, soil-plant-atmosphere. The text is well illustrated with tables, textfigures, and photographs.

The reader meeting the problems of inorganic plant nutrition for the first time may well be impressed with their complexity. For example, mere addition of fertilizer to the soil does not necessarily insure its availability to the plant, as Hoagland carefully points out. A number of factors in the soil, as in the plant, affect rates of absorption and determine whether growth is normal or whether deficiencies of one or more than one element will develop. Many problems for future research are indicated by the author's treatment.

Many will regret—as the reviewer does—that Professor Hoagland did not hold his audience "past the hour" and give his evaluation of other phases of this subject.—NOE HIGINBOTHAM.

THE CARNIVOROUS PLANTS. By Francis Ernest Lloyd. Vol. IX of a New Series of Plant Science Books, edited by Frans Verdoorn. Chronica Botanica Co., Waltham, Mass. 1942. xv + 352 pp., frontispiece, 38 pls., 11 figs. $6.00.

Ever since their discovery the study of the carnivorous plants has captivated botanists. Information concerning these extraordinary plants stems frequently from folklore but includes now detailed biochemical studies on the utilization and importance of animal prey. The mechanisms evolved for this purpose by the many carnivorous plants belonging to widely separated taxonomic groups differ greatly in their efficiency and design. These extremely specialized structures, their component tissues, operation and functions are reviewed on the basis of available accounts and constantly supplemented and appraised in the light of the author's significant observations. For example, Darwin regarded *Dionaea* as the "most wonderful plant in the world," whereas Lloyd is of the opinion that "the evidence seems to favor *Utricularia*." The book then offers the reader a critical summary of our scattered knowledge of these plants as well as a wealth of valuable new information.

The author's delightful style does full justice to the fascinating story of the carnivorous plants and betrays readily his wide personal acquaintance with them. But, regardless of how tempting comparisons with man-made gadgets and anthropomorphic interpretations might have been—a real "pitfall" to many less critical observers—the author wisely refrained from making such efforts by confining his comments to some obvious analogies and by not offering any "explanation" of the origin and evolution of carnivorous plants.—THEO. JUST.

NOTRE DAME MATHEMATICAL LECTURES, Number 4. Alignment Charts, by Lester R. Ford; The Teaching of the Calculus of Probability, by Arthur H. Copeland; On the Relation between Calculus of Probability and Statistics, by Karl Menger; On the Theory of Complex Functions, by Emil Artin. Lithoprinted. Univ. of Notre Dame. 1944. 70 pp. $1.25.

With the movement of many of the biological sciences into the province of numbers and measurements, there arises the necessity of training students to analyze the numerical data in order to formulate and evaluate conclusions. Because of this fact, the wisdom of giving students in genetics, physiology, morphology, ecology, etc. formal training in the methods of appraising numerical data according to modern statistical notions is patent and undebatable, but such wisdom is unfortunately not commonly noted. To the teachers and to some students in the fortunate classes which exist at least two of these lectures will be valuable complements to the textual aids in use in the class. In his article Copeland presents methods for relating statistical data with the theory of probability, and Menger discusses tests for the probability of accuracy of rejection or acceptance of hypotheses set up from observed data. In these articles teachers and students who are not unaccustomed to the mathematician's language and method of presentation may find resolution of some difficulties associated with certain statistical concepts.—E. L. POWERS, JR.

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